Chondrocranium Amphibia Misc. Papers.

Contents

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Earlier Stages.

BY

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THE SKELETAL ANATOMY OF AMPHIUMA DURING ITS EARLIER STAGES.

BY O. P. HAY.

IN the *American Naturalist*, Vol. XXII (1888), p. 315, the writer has published an account of the finding of the eggs of *Amphiuma*, and accompanied it with a short description of the anatomy of the embryos contained in those eggs. In the present paper it is proposed to enter somewhat more into details in describing the structure of the skeleton of the young *Amphiuma* and to illustrate the descriptions by drawings.

As stated in the communication referred to, these eggs were found in a cypress swamp at Little Rock, Ark., on Sept. 1, 1887. They had been deposited in a small excavation under an old log, which was lying at a distance of some rods from the nearest water; and were being cared for by the mother, who was lying coiled up around them. The mass of eggs was about as large as one's fist, and, being connected in strings, they greatly resembled a mass of large beads. When the eggs were put into alcohol, the young were seen to move about within the eggs.

The egg-strings were so entangled that it was found to be impossible to separate them, for the purpose of determining the number of strings and of eggs. However, since there were four ends visible, it is supposed that there were two strings, one for each oviduct. The number of eggs is estimated to be at least one hundred and fifty. They are globular in form, and have an average diameter of 9 mm. (See Fig. 1.) They are separated by from 5 to 12 mm. of string. Fourteen eggs were counted on a piece of string 225 mm. in length. Each egg, in the condition in which they were discovered, consists of the contained larva and an external capsule. This latter is of a condensed gelatinous material, thin as paper, becoming brittle in strong alcohol, but swelling somewhat in weaker alcohol and in water. The connecting cords are of the same materials, and have a diameter

of from 1.5 mm. to one-half that size. The capsules are almost entirely filled up by the young amphiumes; but in their fresh state they probably contained also some water. The young are coiled within the eggs in various positions, so as to form about three turns of a spiral. On being taken from the eggs and extended, they are about 45 mm. in length (Fig. 2). So far as I have been able to discover, they are all at the same stage of development. The color above is dusky, with a slightly darker dorsal streak and a similar lateral band. Below, the color is pale. In the alcoholic specimens the belly appears yellow on account of the great amount of yolk that is contained within it.

In form and proportions the young amphiume is stouter than the adult, and the head is broader and more depressed, and the snout more rounded. The head, therefore, resembles more nearly that of the typical Urodeles than does that of the adult. The eyes also are more conspicuous than are those of the more mature animals, and would doubtless, for some time after hatching, be of more service. The fore and the hinder limbs are present, but are diminutive in size. On the anterior limb, three toes are indicated; the hinder limbs give little evidence of separation into digits. The tail differs from that of the adult, inasmuch as it has on both its upper and lower edges a distinct membraneous fin.

The larvæ possess conspicuous gills; and since they are evidently near the period of hatching, it becomes quite probable that these gills will be retained for some time after the young have betaken themselves to the water, their native element. The gills consist of three pairs, and are of the simply pinnate form. The second gill is the longest, measuring about 9 mm. in length, and gives off from the main stem ten delicate twigs. Only once have I observed any of these lateral filaments to divide. The first and third gills are somewhat shorter, and have about eight lateral branches each. In all the main stems and the lateral twigs may be seen arteries and veins filled with the coagulated blood. Three gill-slits are still open, the first and second of which become closed in the adult.

We cannot but be struck by the close resemblance that exists between the breeding habits of the *Amphiuma* and those of *Epicrium glutinosum* of Ceylon, as these are presented to us by Messrs. P. B. and C. F. Sarasin in the "*Arbeiten aus dem*

Zoologisch-zootomischen Institut in Würzburg," Bd. VII, 1885. According to these observers, the female of *Epicrium* excavates a cavity in the earth a little below the surface, and there deposits a mass of eggs, which are connected by means of an albuminous cord, and thus resemble a string of pearls. These eggs, when found in the oviduct, are of an oval form, about 9 mm. through the longer axis and 6 mm. through the shorter; but, when found in the earth, they were about twice as large, having probably during their development absorbed considerable water. Unlike *Amphiuma*, the eggs seem to have something of a regular arrangement in the mass, the connecting strings being bent in toward the centre of the mass and cohering there into a viscous knot. Around this mass of eggs the female lies coiled, and gives them protection. The embryos at the stage described were 4 cm. long, and moved actively about. On each side of the neck were three plume-like gills, the longest of which was about 2 cm. The eyes were relatively large and distinct; while the tail was surrounded by a strongly developed fin-membrane. These eel-like young must greatly resemble those of *Amphiuma*. Other larvæ of *Epicrium* were found by the Messrs. Sarasin swimming in the neighboring brooks. These are without gills, possessed yet gill-clefts and a caudal fin, and are said to attain a length of perhaps 16 cm. At length their transformation is completed, and they leave the water. These facts bearing on the mode of embryonic development and others derived from anatomical structure have made it evident to the writers named above, as well as to others, that the Cœcilians must be arranged very closely to the Urodela, if not consigned to the same order. The habits of oviposition and incubation and the course of development which have now come to light as characterizing *Amphiuma*, must tend to strengthen this opinion.*

It is not yet known how the young amphiumes get to the water after they have been excluded from the eggs. Considering the nature of the ground where the eggs were found, it would appear impossible for them to travel any considerable distance. It might well be, however, that, like many other

* Dr. C. O. Whitman kindly sends me the interesting information that the Giant Salamander of Japan *(Megalobatrachus maximus)* lays its eggs in a string exactly like that of *Amphiuma*, and the eggs are of about the same size.

Amphibia, their development would be retarded until some fortunate day when a heavy rain would make it possible for them to reach permanent water.

I now proceed to describe the structure of the larval *Amphiuma* as disclosed by the contents of the eggs under consideration. In my attempts to unravel this structure, I have depended partly on dissections made by means of lens and needle, but mostly on stained sections cut and mounted serially.

I. THE SKULL.

In Fig. 3 we have a view of the cartilaginous cranium seen from above, and in Fig. 4 a view of the same from the side. What will probably first strike the attention of the observer is the existence, in the basilar region, of two fontanelles in the cartilage, one on each side of the middle line. They are of an elongated oval form, and are of such size that they leave only a narrow strip of cartilage between them, and a similar ledge along the inner and lower border of each otic capsule. Both before and behind these fontanelles, the cartilage passes from one side of the skull to the other. This portion of the primitive skull is worthy of comparison with the adult skulls of *Necturus* and *Siren*. In *Necturus* the trabeculæ cranii are not connected by cartilage behind the pituitary region, and have but a narrow band connecting them in the exoccipital region; so that there is no cartilage in the floor of the brain-case behind the ethmoidal region until immediately in front of the foramen magnum. In *Siren* there exists, opposite the middle of the otic region, a band of cartilage that passes from side to side. Behind this, there is in the middle line a single fontanelle; and this is limited behind by the cartilage of the basioccipital region. The anterior ends of the two fontanelles of *Amphiuma* come much further forward than does the single one of *Siren*.

In the narrow strip of cartilage between the two basal fontanelles is seen the anterior end of the notochord extending well forward toward the pituitary space.

In the exoccipital region the condyles project prominently backward, after the manner of those of the adult. The deep notch between them is occupied by the tooth-like process of the

atlas. On each side, at the base of the condyles, are the foramina for the vagus and the glossopharyngeal nerves. The occipital condyles are invested with a thin ectostosis, which continues as far forward as the foramina mentioned. This is the only cartilage-bone that is found in the skull, except that in the hyobranchial apparatus, soon to be described.

In the supraoccipital region, there is a narrow strip of cartilage which arises from the posterior end of the otic capsule, and extends inward toward the middle line, but it lacks much of reaching the corresponding cartilage of the other side. Along its upper surface, therefore, the brain, from one end to the other, has no other protection than that of the integument.

The otic capsules are large, well-developed, and of a long-ovoidal form. They occupy about one-third of the total length of the cartilaginous skull. The upper surface is somewhat flattened, and slopes outward and downward. Anteriorly they pass by a narrow band of cartilage into the upper edge of the trabeculæ in front of the foramina for the fifth pair of nerves. Behind, each capsule is rounded, and in the angle between it and the projecting condyle, is found the vagus ganglion. The membraneous canals are well-developed, and may be seen through the walls of the capsule. They are enclosed within corresponding cartilaginous canals. On the outer wall of the capsule is found the large fenestra ovalis. It is partially occupied by the cartilaginous stapes, as shown in Fig. 4. All round this stapes is a tract of membrane, except anteriorly, where it is articulated to the otic wall. This stapedial cartilage is confluent with the hinder end of the columella, which will come up for consideration in its place. With the exception of the fenestra ovalis, there is no interruption in the cartilage of the outer wall of the otic capsule. The facial foramen lies immediately in front of the fenestra ovalis. At the anterior end of the capsule, and on the lower floor, is found the entrance of one portion of the auditory nerve into the labyrinth. Farther back, about opposite the fenestra ovalis, there are three openings in the cartilage of the mesial wall of the otic capsule. The smaller one, high up, is for the passage of the ductus endolymphaticus into the brain-cavity. A second larger foramen in the cartilage, immediately below the last mentioned, admits into the labyrinth the branch of the auditory nerve going to the sacculus and lagena. This

nerve will receive further attention. Immediately behind the foramen just considered is a third break in the cartilage, the purpose of which I have not been able to determine. It possibly gives passage to some of the lymph sinuses.

In sections made previously to decalcification, there are seen abundant otolithic deposits.

In front of the otic capsules, the trabecular walls are low and slope gently downward and inward. The foramen for the branches of the trigeminal nerve is large, and is traversed by the long, slender, ascending process of the suspensorium (Figs. 3 and 4, *As.p.*), which process passes between the orbito-nasal and the other branches of the fifth nerve. Anteriorly to this foramen the cranial walls, becoming lower, approach each other gradually until they finally meet and coalesce, and thus enclose the ovate-acuminate pituitary space. A little further forward, the trabeculæ again separate into the cornua.

In the low trabecular wall, just behind the eye, are found two foramina. Through the most anterior passes the optic nerve. The posterior possibly admits the passage of the oculo-motor; but this I have not been able to demonstrate.

In front of the optic foramen, there is given off from the upper border of the trabecular wall a rod of cartilage which extends outward and forward to a point just in front of the eye, and above the hinder end of the nasal-sac. Here it expands into a rudimentary capsule for this organ (Figs. 3 and 4, *Na.C.'*).

From the point where the above-mentioned rod leaves the cranial wall, the trabeculæ are slender and rod-like, but increase somewhat in size to their coalescence in the ethmoidal region. The lateral halves of the ethmoidal cartilage slope downward and outward. There is no trace of a naso-septal lamina. The trabecular cornua are bilobate, one portion of each (Figs. 3 and 4, *C.t.'*), forming a plate that curves outward under the nasal-sac; the other running forward, at first a little outward, then downward and inward, until it terminates in a point close to the base of the ascending process of the premaxilla (Figs. 3 and 4, *C.t.*).

Just below the eye there is a short piece of cartilage that stands outward and forward from the trabeculæ, to which it is joined by means of connective tissue. This is the antorbital (Fig. 4, *Ant.*). Running parallel with the trabecula along its

outer border, and between the antorbital cartilage and the trigeminal foramen, is a slender club-shaped tract of cartilage, whose position is shown in Fig. 4, *Pt.* It appears to represent the pterygoid cartilage of other Urodeles; but it has not yet formed a connection with the suspensorium. It lies about its own diameter outside of the trabecula.

The eye is wholly devoid of any cartilaginous capsule.

Another cartilage that I have sought for with great interest is that which appears in the roof of the mouth of the adult, in front of and between the anterior ends of the vomers and below the palatine process of the premaxilla. Not a trace of this cartilage is seen in any sections that I have examined.

The floor of the brain-case just described is concave from side to side. Proceeding forward from the foramen magnum, the floor, as shown in a longitudinal section along the middle line, slopes rapidly down beneath the hind-brain, then horizontally forward to the middle of the cerebrum, where the slope is again upward.

Coming to the post-oral structures, we observe first that Meckel's cartilage comes forward and meets its platetrope, while posteriorly it projects behind the articulation with the suspensorium, and gives insertion to the digastric muscle. This cartilage is ensheathed by membrane-bones, which will be considered further along; but it shows no signs of a deposit of calcific matter to form the articular.

The suspensorium (Fig. 4) is of a quadrate form, is directed slightly forward, and in transverse sections is broader below than above. It articulates with the auditory mass by means of the otic process and the pedicle. Starting from the lower end and inner border of the suspensorium is the long and slender ascending process, which runs upward and forward, and coalesces with the cranial wall at the anterior side of the trigeminal foramen. I find no trace of a pterygoid process. From the hinder border of the suspensorium (Fig. 4) starts out a short process which articulates with the columella auris. No ossification has as yet appeared in the suspensorium.

The columella is a short rod of cartilage, which, articulating with the suspensorium anteriorly, runs backward and coalesces with the outer surface of the stapes. Its relation to the facial nerve will be discussed later.

The hyobranchial apparatus (Figs. 4 and 5) consists of the hyoid arch and four branchial arches. The hyoid arch presents, on each side, a hypohyal and a ceratohyal. The basihyal has not as yet become chondrified. There is a single basi-branchial as in the adult. The four branchial arches are much as in the mature animal. There is no second ceratobranchial present. Huxley states that there is one present in the adult, but it is not represented in Wiedersheim's figure. The ossification connected with the hyobranchial arches will be referred to immediately.

Ossifications. — It has been already stated that the exoccipitals are undergoing ossification. These ectostoses do not meet in the lower middle line in front of the foramen magnum.

The only other ossification of this kind occurs in the first branchial arch. A delicate but easily distinguishable layer of bone invests the slender portion of the lower end of the cartilaginous bar, as shown in Fig. 5.

The following parostoses occur in this skull: premaxillary, vomers, parasphenoid, frontals, parietals, squamosals, dentaries, angulars, and a hyoidean splint. In my determination of the presence and the relations of these bones, as well as of the two cartilage bones, I have carefully compared them with the ossifications found in the skulls of larval *Amblystomas*. I have also, in the case of nearly all of them, been able to dissect them out, clean them, and apply chemical tests.

The premaxillary of the adult is a very remarkable bone; it is no less so in the case of the embryo. In the adult the lateral halves are so completely consolidated that no evidence is afforded by them that they ever have been distinct. It is composed of two alveolar processes: an ascending process, which runs backward between the nasals and the frontals to a point a little behind the line joining the anterior borders of the orbits; and a palatine process, which appears in the roof of the mouth between the vomers nearly as far back as their hinder ends and underlying the parasphenoid. It appears to be this process which has been described by several authors as a sphenoidal ossification. For nearly half their length anteriorly these two processes are connected by a thin plate of bone which functions as a nasal septum. Nearly the whole remaining space between them is occupied by cartilage. Dr. Wiedersheim

(*Kopfskelet der Urodelen*) seems to have been the first to describe correctly this structure, especially the relation of the palatine process to the premaxilla. He endeavors to explain this remarkable bone by suggesting that we have in it a composite of morphologically different elements. In the ascending and the alveolar portions of the bone there is supposed to be the proper premaxillary. In the osseous nasal septum and palatine process we have an ectosteal (*perichondrostotisch*) bone formed from the originally hyaline nasal septum, which bone has become confluent with the proper premaxillary. The fact that the parasphenoid pushes itself between the ethmoidal cartilage and the posterior end of the palatine process causes Dr. Wiedersheim to suggest a doubt as to the correctness of his own theory; and he says that amid these doubts nothing will clear up the difficulty except a knowledge of the embryology of this Urodele.

In my specimens the premaxillary is already well ossified; and there is, even in this early stage, no trace of any original separation into two centres. The alveolar processes are long and comparatively strong. Situated on their border is a number of teeth, eleven, as I count them, one being accurately in the middle line. An examination of the adult in my possession shows that it has the same number and arrangement of the teeth. In the young this median tooth, and one on each side of it, are especially large, sharp-pointed, and directed nearly backwards. There are long ascending and palatine processes, although, as might be expected, they do not extend so far backward as in the adult. The palatine process reaches back nearly to the point where the trabecular cornua diverge from each other. It has no connection with any cartilage, and there is at this stage no cartilaginous nasal septum. It seems quite evident, therefore, that the premaxillary is not a composite structure, but that the palatine process continues to grow backward as a membrane-bone until it attains the dimensions that it has in the adult.

As has already been stated, the anterior lobes of the trabecular cornua, like a divided prenasal process, end in the angle between the alveolar and the palatine processes quite close to the lower border of the latter, and close to one another. To me it now appears quite probable that these cartilages grow

downward until they meet below the palatine process and then coalesce. Afterward, by the expansion medially of the maxillaries and the vomers, the portion of the cartilage below the plane of the vomers becomes cut off from the cornua, and forms the unpaired piece that appears so anomalous. But it will require older specimens than those in my possession to settle this matter fully.

The frontals are long, slender splints which first appear, posteriorly, in those cross-sections which pass through the hinder border of the eye. At their hinder ends they are comparatively thick, and overlap the parietals. They lie entirely above the level of the eyes. At the anterior border of the eyes, the frontals descend to near the level of the cartilage overlying the nasal-sac, the lower edge lying a little nearer the middle line than the upper border of the nasal-sac. They may be traced forward as very thin films as far as the perpendicular section just in front of the divergence of the trabecular cornua. Such sections show the anterior end of the cerebrum, and the hinder ends of the two median processes of the premaxilla. (See Fig. 6.) This anterior end of the frontal passes forward over the olfactory nerve, which is directed laterally into the nasal-sac, and the bone may be followed to the anterior border of the nerve. Wiedersheim (*op. cit.*, pp. 52–53) has shown that the anterior end of each frontal forms a sort of ring or ferrule (*Knochenzwinge*) around the olfactory nerve, and through which this nerve makes its exit from the brain-cavity. According to his descriptions, there is a flat process of bone sent down from the frontal on the outside of the nerve; then in front of this outer process a similar one descends on the inner side of the nerve; then the two are united under the nerve. Already in my specimens the frontal has come into close relations with the nerve, but has not yet enclosed it by means of its processes.

The parietal extends from the perpendicular sections through the hinder border of the suspensorium forward to that passing through the anterior border of the lens. It is better developed than the frontals. Its lower border lies upon the upper border of the auditory capsule and trabecula to the eye, where it rises somewhat above the cartilage. In the latter region also it lies somewhat below the hinder end of the frontals.

Neither the frontals nor the parietals, along their inner or upper borders, approach at all near the middle line.

The vomers, or vomero-palatines, are present as a pair of thin, narrow splints, which extend from the middle of the subnasal bands of cartilage backward almost to the antorbital cartilages. They lie parallel with the trabeculæ and a little outside of them. Each is accompanied by a row of dental papillæ, five or six in number. These lie a little to the mesial side of the bone. Some of the papillæ are already undergoing calcification.

There are no deposits of bone to represent the maxillæ; but two rows of tooth-papillæ, five or six in each, which extend backward from the hinder ends of the alveolar processes of the premaxillæ, show where these maxillæ will soon appear.

No bony pterygoids, prefrontals, or nasals are yet to be seen.

The parasphenoid is a broad but very thin and delicate film of bone underlying the brain from just in front of the foramen magnum forward nearly to the coalescence of the trabeculæ, and passing laterally from one trabecula to the other.

The squamosal is a curved bone that overlies the suspensorium and runs upward and backward upon the otic capsule. Its lower border is applied closely to the columella along the anterior half of the latter.

The lower jaw is furnished with two strongly developed bones. One of these is the dentary. It meets its fellow in front to form a symphysis, and extends backward on the outer side of Meckel's cartilage nearly to the articulation with the suspensorium. Arranged along each dentary are about fifteen teeth, only the anterior one of which is anchylosed to the bone. This tooth and the one immediately following it are large and fang-like, and correspond in that respect to the large teeth of the premaxillary.

The second bone of the mandible, the angular, lying along the inside of the cartilage, extends from the angle of the mandible half way to the symphysis.

There is no trace of a splenial bone, and none of an articular.

As before stated, there is a parostosis connected with the ceratohyal. It lies along the inner and lower side of the cartilage, running nearly the whole length of the latter. This slender splinter of bone I have repeatedly been able to dissect off; and having under a cover-glass treated it with hydrochloric acid, have obtained satisfactory effervescence. Wiedersheim (*op. cit.*, Tafel I., Fig. 8) represents the ceratohyal as having a strip of

bone running its length; and an examination of the adult at hand shows that the cartilage is only partly ensheathed by bone.

The lower end of the first branchial arch is meanwhile undergoing ossification of a different kind, being overlaid, as before mentioned, with bone deposited ectosteally.

To the foregoing on the cartilaginous and bony skull, I make the following notes on other structures belonging to the head: —

The common ganglion of the facial and auditory nerves lies wedged in between the otic capsule and the outer bar of the basicranial cartilage. It gives origin, as usual, to the facial nerve, which runs outward to escape by the facial foramen, and to the auditory, which enters and supplies the anterior portions of the labyrinth. Further back the ganglion, or what appears to be a portion of it, seems to be crowded through the mesial wall of the capsule so as to appear to lie partly within the capsule. Here it lies in close relation with the mesial wall of the sacculus, to which it distributes nerve-fibres, as it does also probably to the rudimentary cochlea. This branching of the auditory nerve before it enters the capsule I have observed also in *Amblystoma* and *Spelerpes*. The acoustic nerve in the frog enters the labyrinth by two or more foramina (Owen, *Anat. Vert.*, Vol. I, 312).

The facial nerve, after emerging from the cranial cavity, courses outward and passes below the columella. My sections show this plainly. Dr. Wiedersheim undoubtedly errs when he announces (*op. cit.*, p. 137) the rule that the facial nerve in all Urodeles, without exception, makes its way out over the suspensorio-stapedial ligament, whether this consists of fibrous tissue or cartilage. And unless the relation of the facial nerve to the columella in *Menopoma* is variable, it, too, offers an exception to his rule, despite the figures which he gives to illustrate these parts (*Kopfskelct*, etc., Fig. 24). Messrs. Parker and Bettany (*Morphology of the Skull*, p. 132) state that the cartilage passing between the stapes and the suspensorium lies *over* the facial nerve, and a dissection made by myself is confirmatory of this statement.

Mention has already been made of the foramen of the ductus endolymphaticus. This latter is a narrow tube which enters the brain-cavity, having taken its origin in the sacculus. On the upper and outer surface of the brain it expands into a saccus

endolymphaticus of considerable size; but those of the opposite sides do not come into contact.

There are at this stage rudiments of two nasal glands. Each consists of a single duct, which opens into the floor of the corresponding nasal-sac and passes directly inward so as to lie finally upon the outer edge of the anterior end of the ethmoidal plate. Here it divides into two tubes, which may be traced for a short distance backward along the inner side of the nasal-sac.

II. The Axial Skeleton.

The vertebræ are undergoing ossification, and this is more advanced in the anterior, than in those of the pelvic, region. The bodies of the vertebræ are invested with a layer of bone which closely surrounds the notochord. Toward the ends of the vertebra the bony sheath expands a little, so that the vertebral body is somewhat hour-glass shaped. There is in the centre of each vertebral body a portion of vertebral cartilage, as represented by Dr. Wiedersheim in his *Comparative Anatomy* as belonging to the vertebra of *Gyrinophilus porphyriticus*. Outside the notochordal sheath, at the ends of each vertebra, is a ring of much-modified intervertebral cartilage. The cartilaginous arches of the vertebræ come down upon the bony sheath of the centra, and the bone rises up from the centra upon these arches two-thirds the distance to their upper ends.

There are no traces of ribs. Above the base of each lateral half of some of the anterior vertebral arches there stands out a process to which the future rib will possibly be attached.

III. The Appendages.

The shoulder girdle consists of two lateral masses of cartilage, in each of which may be distinguished a scapula, a coracoid, and a precoracoid. The scapula is slender, and is directed downward and forward. The precoracoid is somewhat longer than the coracoid. Both are considerably broader than the scapula. They are widely removed from each other in the middle line below. There is no suggestion of a sternum.

The humerus has its shaft ensheathed in a thin layer of bone.

The ulna and radius, carpal, metacarpal, and phalangeal elements are present in cartilage.

The pelvic girdle consists of a plate of imperfectly differentiated cartilage on each side, which has no connection with the vertebral column above nor with its fellow below. Femur, tibia, and fibula are present in cartilage, as well as some portions of the foot.

IV. OBSERVATIONS ON A LARGER SPECIMEN.

Since the above was written, I have received from the collections of the United States National Museum a specimen of *Amphiuma* six inches long, one of the smallest in the collection. This has been secured in the hope that it might throw some light on the origin of certain structures which had not yet made their appearance in the very young, and might furnish, in the case of other structures, stages intermediate in development between those of the already described larva and those of the adult. Of such structures the most interesting, perhaps, are the unpaired piece of cartilage which is found in the roof of the mouth, and the various portions of the premaxillary bone. The specimen has been decalcified, stained, cut, and mounted serially; and such results as I have been able to obtain are now presented.

As might have been anticipated, this specimen is already too far advanced in development to be of the highest value for the solution of the problems before us. The skull is nearly as thoroughly ossified as it is in the adult. Nevertheless, the preparation is, I think, a very instructive one.

An examination shows that the cartilage which was found in the hinder part of the floor of the brain-case of the unhatched larva has been extensively removed, so that there is now none of this tissue in the middle line between the ethmoidal plate and the narrow basioccipital cartilage. The base of the skull, therefore, as regards the primordial elements, is much like that of *Necturus*, except that such cartilage as remains along the borders of the otic capsules is more extensively ossified in the *Amphiuma*. In the region about the anterior end of the proötic, where in the larva a band of cartilage is sent from side to side, a shelf of bone, now a process of the proötic, extends in-

ward from one-third to one-half the distance to the middle line. On this shelf is supported the trigeminal and facial nerve ganglia. With the central band of cartilage have disappeared also all traces of the notochord from the base of the skull.

The proötics are quite thoroughly ossified. Two points, however, as Wiedersheim has observed, even in the adult, remain in a cartilaginous state, viz.: those to which are articulated the pedicle and the otic process of the suspensorium. A broad band of cartilage, running transversely through the otic capsule in the region of the fenestra ovalis, separates the proötic from the opisthotic. The latter send inward toward the middle line each a process of bone which grows wider as we proceed backward. These, however, nowhere come into contact, but are connected by a considerable basioccipital cartilage.

The foramen magnum is bounded above by the opisthotics, which for a short space come into contact in the middle line. More anteriorly, beneath the hinder ends of the parietals, the opisthotics are separated by a mass of cartilage which may be regarded as the supraoccipital.

The inner wall of the auditory capsule is well ossified. In this inner wall I find anteriorly a foramen for the branch of the auditory nerve, which is distributed to the upper portions of the labyrinth. Further back, a much larger branch of the auditory nerve enters the labyrinth through about three closely placed foramina, and is distributed to the sacculus and probably the lagena. On the inner wall of the sacculus, we find a large macula, and immediately outside of this a very large otolith. (See Fig. 10, *Ot.*) This otolith reminds us of that of some of the fishes. The opening for the escape of the ductus endolymphaticus is situated at the upper border of the wall immediately above the foramina for the saccular branch of the auditory nerve. Just behind the last-mentioned foramina is an opening in the cartilage, as in the larva, through which I have supposed a lymph sinus to pass. This foramen lies just mesiad of the lagena.

The ossification of the trabecula lying mesiad of the proötics is carried forwards, anterior of the foramina for the escape of the fifth nerve. It soon, however, becomes reduced to a mere shell of bone surrounding the cartilage. Then begins the orbitosphenoidal bone. This is more or less completely ossified as

far forward as the section passing through the lens, at which point the frontals and the vomero-palatines begin to enter into the side walls of the brain-cavity. Contrary to Dr. Wiedersheim's statement concerning the orbitosphenoidal bone in the adult, it is in my specimen higher in front than behind.

Following the trabecular walls forward, we find that before the ossifications have disappeared the cartilage has divided itself into two bars, an upper and a lower, corresponding to those of the larva, which are designated by *Na.C'* and *Tr.* in Figs. 3 and 4. The lower bar is the continuation of the trabecula. Opposite the eye, the upper bar is a very slender rod, which does not lie nearly so far to the outside of the middle line as it does in the embryo, a circumstance due probably to the narrowing of the snout. As soon as the nasal-sac is reached, this rod expands outward, while its inner edge lies against the descending process of the frontal bone. Just where the olfactory nerve pierces the frontal, the cartilage again divides into an inner and an outer portion. The inner division runs forward in the angle between the facial and the descending processes of the frontal and coalesces with the **X** of the cartilaginous nasal septum. The outer division extends forward over the upper outer side of the nasal-sac until opposite the bony internasal septum, where its outer edge unites with the cartilage that underlies the nasal-sac; its inner edge meanwhile extending inward meets and unites with the advancing border of the cartilage that covered the inner and upper wall of the nasal-sac. In other words, we may say that the nasal-sac is roofed over with a cartilage that has in it a large fontanelle, and that this roof mesially coalesces with the cartilaginous nasal septum, while externally it coalesces with the band of cartilage which expands beneath the nasal-sac.

Where the internasal septum is formed by the premaxilla, the cartilage is missing on the inner side of the nasal-sac, but above, below, and on the outer side, the cartilage is unbroken. When the alveolar process of the premaxilla is reached, no cartilage is found immediately over it; but on the outside of the sac and above it, the cartilage continues to the borders of the external nostrils, while just before the nostril is reached, the cartilage is expanded so as almost to surround the passage.

On its lower inner side the nasal cartilage sends a prong into the angle between the body and the alveolar process of the

premaxillary, as has been shown in the case of the larva. Below the premaxillary is found the unpaired piece of cartilage which has already been referred to. There is no cartilaginous connection between it and the processes from the nasal cartilages ending in the angle between the body and the alveolar processes of the premaxillary. Hence, my theory of the origin of the unpaired cartilage is not demonstrated by the specimen in hand. However, it is not disproved; while the apparently transitional character of the intervening tissues is favorable to the opinion that the cartilage has but recently undergone conversion into connective tissue. It is greatly to be desired that a specimen of this species may soon be obtained of intermediate age, so that the origin of this structure may be definitely determined.

The premaxillary has the same features as that of the adult. I can, however, see no grounds for accepting Dr. Wiedersheim's view as to the origin of the median descending plate and the palatine process from the interseptal cartilage. There is nowhere to be seen such a transition from bone to unossified cartilage as might be expected, were the bone derived from the cartilage. The relations between these portions of the premaxillary are no more intimate than is that between these cartilages and the descending processes of the frontals. There is thus no sphenoidal ossification in this animal.

It appears to me that many of the peculiar structures of the *Amphiuma* may be explained by considering its habits. It is eminently a burrowing animal, as has been shown by many observers. Such a mode of life would require and, in time, lead to the production, probably, of a narrow and pointed snout, instead of the rounded snout, so common among the Urodeles. The ability to thrust the body rapidly into the earth at the bottoms of rivers and swamps would also call for a solidly constructed cranium; and accordingly, we find the skull of the *Amphiuma* as thoroughly ossified as in the higher members of its order. In the act of burrowing the premaxillary would be especially exposed to pressure, and it would be essential that this pressure should be transmitted to and sustained by the other bones of the skull. This result is secured in a beautiful and effective manner through the structure and connections of the premaxillary. Its solidity is, first of all, secured by its being composed of but a single piece. At the sides its alveolar

processes are joined to the strong maxillaries, which, instead of being directed widely outward, as in *Cryptobranchus*, are turned backward with their palatine processes lying close to the long and strong vomers. The latter, in their turn, run far back beneath the parasphenoid, and all these bones are firmly bound together by connective tissue. On the upper surface of the skull, too, the maxillary is closely joined to the nasal, and through the prefrontal with the strongly developed frontal. This, however, seems not to be enough. The premaxillary has, above, a process that extends back between the nasals and ends by being wedged in between the frontals for half their length. Below, the premaxillary sends backward a similar spine, which is firmly bound to the vomers and the parasphenoid. The premaxillary is further strengthened by having the two backwardly directed spines connected at their bases by the plate of bone which functions as a partial internasal septum. The whole structure of the skull is in strong contrast to that of the skulls of *Necturus* and *Siren*, both exclusively swimming animals.

Reference has already been made to the peculiar structure of the anterior ends of the frontals, as these have been described by Dr. Wiedersheim. My observations on my largest specimen do not wholly confirm his descriptions. I do not find that the frontal forms anything that can properly be called a ring or ferrule around the escaping olfactory nerve. That the olfactory nerve does leave the brain-case through the frontal is very true. What I do find is this: the anterior ends of the frontals send down each a descending process, which at length touches the ethmoidal cartilage. For a space the processes form the side-walls of the brain-case, and when they have come into contact, they function as a portion of the internasal septum. Where they form the walls of the cranium, the olfactory nerves of course lie mesiad of them. As the processes approach each other like the sides of a wedge, the nerves at length pierce them and enter their respective nasal-sacs. Fig. 7 represents a section made across the head at the point where the nerves are either passing or are about to pass through the frontals. On the right the olfactory foramen has not yet been reached, though the bone is thinning. On the other side the nerve is in the act of escaping through the process. Fig. 8 shows the condition of things only two-thousandths of an inch further forward. Here

we find both nerves on the outside of the descending processes, and yet these processes have undergone no change, except that they have approached each other more closely. These parts may undergo some modifications by the time the animal has reached adult size, so as to justify the distinguished author's description, and his Fig. 20, Tafel II; but it seems more probable that he has been misled by not having closely consecutive sections. With my sections the thousandth of an inch in thickness I have no difficulty in making out the changes in position of the processes. It would almost appear that in the process of lengthening which the snout has undergone the orbitosphenoid and the cartilaginous internasal septum have not been able to keep pace with the other structures, and that their deficiencies have had to be made good in the one region by an extraordinary development of the frontals and in the other by the production of the perpendicular plate of the premaxillary.

Dr. Wiedersheim (*op. cit.*, p. 136) states that "das cartilaginöse Operculum zu einem kurzen ebenfalls knorpeligen Stiel auswächst," etc. My specimen, young as it is, tells a different story. The rim of the operculum is wholly cartilaginous; but both the inner and the outer surfaces of the central portion of it are converted into bone. The head of the columella is coössified to the centre of the operculum; but almost immediately after it has freed itself, the columellar rod becomes cartilaginous. The thickened lower border of the squamosal then descends upon the columella, and is continued upon it to a point somewhat in front of the fenestra ovalis. Here this rod once more becomes surrounded by bone, which passes forward into that of the quadrate. *Sta.* in Fig. 10 points to the bone-incrusted operculum. From the anterior bony portion of the columella a broad process of bone rises up between the squamosal and the otic capsule; and this may be traced backward and upward for some distance, until at length it ends in a point. The termination of this point may be seen in Fig. 10, *Co.p.* For a part of the way anteriorly this process rises nearly to the upper border of the squamosal. Such is seen to be the case in Fig. 9, which passes through the foramen for the facial nerve. Here the axis of the columella is seen to be cartilaginous, but surrounded by bone which passes into a plate lying inside the squamosal. We might say, in other words, that the quadrate

sends upward and backward a strong process between the squamosal and the otic capsule, and that the lower border of this involves the greater portion of the columella. As far forward as the quadrate the squamosal rests on the columella, the process just mentioned springing from the inner border of the columella. This relation is shown in Fig. 9.

If we consider how firmly the quadrate is clamped to the skull by means of the squamosal, how greatly movements of the columella must be restricted by its close connection with the squamosal, and how the backwardly directed process of the quadrate adds to the stability of the parts, we can easily believe that the delicate structures of the labyrinth will be but little disturbed by movements, even the most violent, of the jaws. Since the *Amphiuma*, as has been shown both by the observations of Dr. Shufeldt (*Science*, Vol. II, 163) and myself, attacks its enemies with great vigor, seizing them between its jaws and turning about its long axis like a drill or whirling around in a spiral, it would appear necessary to protect the delicate organ of the ear from such agitation as might during such conflicts be imparted to it through the columella.

The facial nerve is plainly seen to escape beneath the columella. This is shown in Fig. 10, *VII*.

The principal part of the ossification of the quadrate is found on the outer surface of the cartilage. It is overlapped by the squamosal, and along its outer border sends out a ledge which supports this bone. The remarkable process sent backward by the quadrate has already been mentioned. It may be called the columellar process of the quadrate.

The pterygoid cartilage, which in the larva consisted of a slender rod unconnected with the suspensorium, has now joined the lower border of the ascending process about one-third of the distance back of where the latter unites with the trabecular cartilage. The pterygoid bone is present as a very thin and slender splint, which posteriorly forms a suture with the inner side of the quadrate, and runs forward beneath first the ascending process of the suspensorium and then the proper pterygoid.

Posteriorly the groove for the temporal muscle and tendon is along the lower border of the parietal bone. When the proötic bone is reached, the parietal overlaps it. Farther forward the two bones form a harmonia suture. Near the anterior end of

the labyrinth the proötic rises so as to overlap the parietal, and at length it alone forms the outer wall of the groove. This process of the proötic continues thus to its termination at the very tip of the beak-like process of the parietal, which Wiedersheim has figured on Tafel II, Fig. 17.

The antorbital is almost entirely cartilaginous, but posteriorly coalesces with the ossification of the orbitosphenoid.

I find no cartilage strengthening the capsule of the eye. While such a support seems usually to be present in the eye of the Urodela, I find none in that of *Spelerpes longicaudus*. The integument passes over the eye of *Amphiuma*, and the connective layer is very dense and thick. The animal probably enjoys very limited powers of vision.

In the lower jaw we find the articular undergoing ossification; but this seems to be due rather to an extension of the bone of the angular first around, and then into, the territory of the articular, than to an independent centre.

As already observed in the case of the larva, the ossification of the hyoid seems to be rather a parostosis than a cartilage bone. The bone lies on the mesial side of the cartilage. At the anterior end of the hyoid, the bone seems almost immediately to press itself through the cartilage, so that there is cartilage on both sides of the bone. Further back, the bone thickens, becomes crescentic in section, and partially encloses the outer and main portion of the cartilage. In Fig. 9 at *Ce.h.o.* I have represented the section and position of this bony portion of the hyoid. The letters *Ce.h.c.* point to the portions of the cartilage. These relations continue nearly to the upper end of the hyoid. For the greater distance, the cartilage on the mesial side is a very slender rod, and at one point it disappears entirely, but almost immediately it comes into view again. As there is no trace of this inner rod of cartilage in the larva, it must grow from the extremities of the outer cartilaginous rod. Near the posterior end of the hyoid, the two portions of the cartilage reunite into one mass.

About the ends of the hypohyal are located several nodules of cartilage, which probably represent the basihyal. Dr. Wiedersheim has figured these as he has observed them in the adult.

A large portion of the basibranchial is ossified. The first branchial arch is ossified from end to end. Here, as in the case

of the basibranchial, the caleific deposit forms a shell surrounding the rod of cartilage, but the deposit is also invading the cartilage extensively.

For the opportunity of making my investigations on this extremely interesting animal, I am indebted to Dr. John C. Branner, Director of the Arkansas Geological Survey, and to the liberality of the management of the National Museum.

EXPLANATION OF LETTERS USED IN THE FIGURES.

Ant.	Antorbital.
As.p.	Ascending process of suspensorium.
Bbr.	Basibranchial.
B.c.	Middle strip of basicranial cartilage.
Br. I, II, III, IV.	Branchial arches.
Br.	Brain. [Rhinencephalon.]
Ce.br.	Ceratobranchial.
Ce.h.	Ceratohyal.
Ce.h.c.	Ceratohyal cartilage.
Ce.h.o.	Ceratohyal ossification.
Co.	Columella.
Cond.	Condyle.
Co.p.	Columellar process of quadrate.
C.t.	Cornu trabeculæ, anterior lobe.
C.t.'	Cornu trabeculæ, lobe beneath nasal-sac.
D.p.	Dental papillæ.
Eth.	Ethmoidal cartilage.
Fr.	Frontal bone.
I.	Olfactory nerve.
II.	Optic foramen.
III.	Oculomotor (?) foramen.
Ma.	Maxillary bone.
Na.c.	Cartilage roofing nasal-sac.
Na.s.	Nasal-sac.
Not.	Notochord.
Ot.	Otolith.
Pa.	Parietal.
Pmx.a.	Alveolar process of premaxillary.
Pmx.n.	Ascending process of premaxillary.
Pmx.p.	Palatine process of premaxillary.
Pr.f.	Prefrontal.
Pro.	Proötic.
Ps.	Parasphenoid.
Pt.	Pterygoid.
S.c.	Semicircular canal.
Sq.	Squamosal.
V.	Fifth nerve and foramen.
VII.	Facial nerve and foramen.
VIII.	Auditory nerve.
VIII.'	Saccular branch of VIII nerve.
Vo.	Vomers.
X.	Foramen for vagus nerve.

EXPLANATION OF PLATE II.

FIG. 1. View of two eggs, containing young and showing the connecting cords.

FIG. 2. View of the young taken from the egg, and enlarged to twice the natural size.

FIG. 3. View of the cartilaginous skull of the larva, as seen from above. Enlarged 10 diameters.

FIG. 4. Same skull seen from side. Enlarged as Fig. 3.

FIG. 5. Hyobranchial apparatus. Enlarged 10 diameters.

FIG. 6. Transverse section across the snout of the larva. Enlarged 56 diameters.

FIG. 7. Section across the snout of the larger specimen, six inches long. This is designed to show the relations of the descending processes of the frontal bone to the olfactory nerves. The nerve is seen, on the left side, passing through the descending process. One branch is passing outward to the walls of the olfactory organ. The section is cut somewhat obliquely, so that on the right side the olfactory nerve yet lies mesiad of the descending process. Enlarged 32 diameters.

FIG. 8. Section taken $\frac{2}{1000}$ of an inch anterior to the preceding. Both nerves have passed through the frontals, but the processes continue on with little change. Enlarged 32 diameters.

FIG. 9. Section across head of same individual as the last. Passes through the foramen for the facial nerve. This figure illustrates the ossification of the columella, and the broad process of bone that arises from it and passes up between the squamosal and the proötic. The ceratohyal ossification lying between the two portions of cartilage is seen, as well as the ossification of the first ceratobranchial. Increased 32 diameters.

FIG. 10. Section through same skull and with the same enlargement. It passes through the anterior edge of the stapes. Shows more especially the columella, cartilaginous at this point, the facial nerve passing below it, the posterior extremity of the columellar process of the quadrate, and the passage of a portion of the saccular branch of the eighth nerve into the labyrinth, and the large otolith.

Figs. 5, 6, 7, 8, 9, and 10 were outlined under the camera and the details filled in from the slide under higher power. Figs. 3 and 4 were partly drawn under the camera and partly reconstructed from the sections.

THE HEAD OF AN EMBRYO AMPHIUMA.

By J. S. Kingsley.

The following is a preliminary account of some studies of a single stage of *Amphiuma means* before hatching. For the material I am under great obligations to Prof. O. P. Hay, of Irvington, Indiana. I must also return my thanks to Prof. Dr. Robert Wiedersheim, in whose private laboratory in the University of Freiburg i-B., my studies were conducted. Only one who has enjoyed the privilege of working with him can appreciate his many kindnesses and extreme helpfulness.

External appearance.—The general appearance of the eggs has already been described by Dr. Hay, and is strikingly similar to that of Ichthyophis as described and illustrated by the cousins Sarasin. This resemblance is strengthened by the fact that the cord connecting the eggs is spirally twisted as in the Ceylonese Gymnophione described by them.

The external description of the embryo Amphiuma has been correctly described by Hay in most points, but in a few respects my specimens differ from his description. According to him "the gills consist of three pairs, and are of the simply pinnate form. . . Only once have I observed any of these lateral filaments to divide. . . Three gill slits are still open." The figures which illustrate this are strikingly like those of the Sarasins of the branchiæ of the Ichthyophis larvæ. In the larvæ which I studied the resemblance is not so striking. The three gills of either side are united at the base into a common trunk, the gill filaments are not bipinnately but irregularly arranged, and in none of my specimens have I found more than one gill cleft open. (*Cf. infra.*)

Chondrocranium.—The cartilaginous skull, as it appears in a wax reconstruction after Born's method (and compared with dissections), is more slender than in Hay's figures; it also presents minor differences in several other respects from his rep-

resentation and description, to which reference should be made in reading the following account:

In front of the pituitary space the trabeculæ unite into a broad horizontal plate, the line of junction of the two halves being entirely obsolete, while still farther forward the cornua trabeculæ, instead of being two-lobed, form a broad triangular plate. Between the two cornua is a deep and narrow notch with parallel sides in which is imbedded the septum osseum of the premaxilla to be described below. The trabeculæ, on either side of the pituitary space, are high and compressed. Just behind the nasal capsules two processes are given off on either side. The upper one, arising from the trabecular crest is, as Hay calls it, the rudimentary nasal capsule, and in one specimen upon one side I found a perforation in this process which suggests the more extensive fenestration in the nasal cartilage of the adult Necturus and Protopterus. The lower process may retain the name, antorbital, usually applied to it, for Amphiuma presents no evidence that it is the palatine cartilage as Gaupp interprets it.

Somewhat farther behind these processes than in Hay's figure are two openings through the trabeculæ for the passage of the optic and oculomotorius[1] nerves.

The trabeculæ are united to the posterior portion of the cartilaginous skull by three processes. The upper connects the crista trabeculæ with the ear capsule; the middle, the process ascendens of Stöhr and other authors, goes from the trabeculæ to the inner anterior angle of the quadrate; the third, the radix trabeculæ, is bifurcate posteriorly, the outer ramus joining the floor of the otic capsule, the other uniting with the parachordal floor of the cranial cavity.

The parachordal cartilage lies beneath the notochord, as do the lower arcs of the occipital and first cervical vertebræ. Between the parachordals and the otic capsule on either side is a large oval opening in the cranial floor. The occipital vertebra is confluent below with the parachordal cartilage; on

[1]Hay suspected that the posterior of these foramina was for the transmission of the third nerve. I have traced the nerve from its origin, through the opening, into the proper eye muscles.

either side it merges with the posterior angle of the otic capsules; above it is incomplete. Between the ventral portion of the occipital vertebræ and its lateral union with the otic capsule is the foramen for the vagus nerve.

The otic capsules are elongate oval. In front they project slightly beyond the point of union with the cristæ trabecularum, behind they merge into the occipital vertebra. In the lower outer surface is the large oval foramen ovale, and just in front of it is the external opening of the foramen for the facialis. This foramen does not penetrate the ear capsule proper, it only passes through its anterior wall. On the inner lower surface the otic capsule is produced into a narrow ledge which projects inwards to form a part of the floor of the cranial cavity, being limited internally by the large opening between it and the parachordal cartilage. The inner wall of the capsule is perforated by three subequal openings in the same plane, and a fourth smaller one above them and between the two posterior ones. The anterior of these forms a considerable cavity, in which is situated the acustico-facialis ganglion and from it nerves go through the adjacent cartilage in the following directions: One branch, the ramus palatinus, goes ventrally through the floor; a second, the facialis proper, goes straight outward to reappear, as just mentioned, upon the outer surface; while the third, the ramus vestibularis of the eighth nerve, goes upward and backward to the sensory epithelium of the inner ear. Separated by a considerable cartilaginous interval from the first of these openings is a second, nearly equal in size, through which the ramus cochlearis of the auditory nerve enters the ear; the small upper opening permits the ductus endolymphaticus to pass above the brain in the same manner that the ductus perilymphaticus goes through the fourth opening beneath the brain. I have seen no special opening in the cartilage for the passage of blood-vessels to the inner ear.

Cartilaginous Visceral Skeleton.—The quadrate is rhomboidal in outline when viewed from the side, the external surface exhibiting a slight depression. As yet it is connected with the skull by only the process ascendens, the processes

oticus and palatobasale being as yet undeveloped. Behind, from the posterior angle, is a projection with which articulates the cylindrical process opercularis (columella), the posterior end of which is imbedded in the still membranous opercular membrane (stapes of Hay), which closes the foramen ovale. Meckel's cartilage articulates with the lower angle of the quadrate, a process extending behind the articulation, for the insertion of the digastric muscle. The two halves of the lower jaw are united by fibrous connective tissue in front. I find no trace of Hay's pterygoid cartilage. The hyoid and branchial arches call for no remark aside from the fact that they lack the yoke which binds together the upper ends of the branchial bars in Amblystoma embryos, and, according to Stöhr, in some other forms.

OSSIFICATIONS.—These have been well described by Hay and only a few words are necessary. The ossifications are here, as Weidersheim has pointed out for all urodeles, perichondrostoses. They consist of, in the cranium at this stage, premaxillary, vomeropalatines (better dermopalatines), parasphenoid, frontals, parietals, squamosals or tympanics, occipital and small patches surrounding the exits of the vagus nerves. In the lower jaw dentary and angular bones are seen, while ossification occurs on the hyoids. The premaxillary at this comparatively early stage shows no trace of a double origin, either in front or in that median osseous process extending backwards, which separates the two nasal cavities. This is the septum osseum of Weidersheim, and is clearly a portion of the premaxillary. It is also, I think, the same bone which Cope has called ethmoid, and upon which both he and the Sarasins have placed great weight in their association of the Gymnophiona with the Amphiumidæ. The squamosal of Amphiuma is clearly not homologous with that bone which Weidersheim (and following him Cope) has called by that name in the Cæcilians, but to which the Sarasins have applied the name jugal. The ossification of the occipital region is peculiar. As is well known the occipital region of the urodele skull is formed by the junction of a primitively separate vertebra with the parachordals and otic capsules. In this vertebra, above its carti-

laginous lower arch and in the fibrous connective tissue on either side of the notochord is a deposit of bone of such a character as to suggest the existence here of an earlier vertebral centre which has disappeared.

VISCERAL CLEFTS.—My specimens are too old to throw any light upon the mooted question of an obsolete visceral segment between mandible and hyoid, but in the region behind the last branchial cleft of the ordinary Amphibian some interesting facts are seen. A reconstruction of the floor of the throat after the method of Born shows the following clefts distinctly:—*a*, the hyomandibular or spiracular cleft, which like *b* and *c*, the first and second branchials, is not open to the exterior; *d*, the third branchial cleft which is still functional, opening to the outer world as already described in referring to the external appearance. Behind this last cleft comes the fourth cartilaginous gill arch; and still behind this and between it and the trachea are two other pits, clearly serially homologous with the others, and hence to be regarded as the representatives of the two posterior clefts of the typical elasmobranchs and ganoids. Of these the anterior (fourth branchial) has already been recognized as occurring in the Amphibian ontogeny; it is the "Suprapericardialkörper" of authors, which Maurer has shown to be the fourth gill cleft. The posterior, the fifth gill cleft has not before been recognized in the Batrachia. These posterior clefts bear such relationships to the trachea as to lend countenance to that view which would derive lungs and trachea from modified gill slits. Should this view ever be substantiated, it may be that the laryngeal cartilages will be shown to be the modified gill-bars of this region. Amphiuma, however, throws not the slightest light directly upon the phylogeny of these structures.

In this connection I may state that in the early Siredon stage of *Amblystoma jeffersonianum* the posterior (fourth) branchial cartilage is bifid at its upper and posterior extremity[2] in such a manner as to suggest that there was formerly here an additional arch, the traces of which are disappearing in the same way in which the posterior gill of Ichthyophis is

[2]This, of course, bears no relationship to the bifid ceratohyals of the ganoids.

merged with its predecessor. In Amphiuma I find no trace of any gill bar behind the fourth of the adult.

NERVOUS SYSTEM.—The brain of the larva studied varies considerably from that of the adult as described by Osborn. The account of the internal structure is reserved until later. Externally it is characterized by its shortness and longitudinal compression, this being more marked than in any adult Batrachian except that of the Gymnophiona as described by Waldschmidt and Burckhardt. It exceeds in this respect the brain of Protopterus as figured by Fulliquet. As in the latter form the cerebral hemispheres are pushed back upon and wedged apart by the twixt brain, while behind, the mid-brain and cerebellum are so folded over upon the medulla that the lateral angles of the 'fossa rhomboidalis' extend nearly to the posterior lobes of the cerebrum.[3] The brain flexure, however, is apparently slight, the primary bend being corrected by a secondary one. The cerebral hemispheres are distinct above and in front of the lamina terminalis; the olfactory lobes are not distinct from the hemispheres. The floor of the twixt brain is very short and the infundibulum and hypophysis are very broad, the latter being wider than the mid-brain in its widest place. The choroid plexus of the anterior ventricles is well developed, but calls for no special remark. The cavity of the pinealis is still in connection with the cavity of the brain and its enlarged distal portion, which reaches nearly to the roof of the cranial cavity, is considerably lobed and folded.

The olfactory nerve arises by a single root,[4] goes laterally from the tip of the hemisphere and, in the nasal capsule, divides into upper and lower branches which innervate the nasal epithelium and Jacobson's organ respectively.

The optic and oculomotor nerves call for no comment. I failed to find the fourth (trochlearis) and the sixth (abducens) in my preparations.

The fifth nerve presents several features of interest. As my

[3]Cf. Waldschmidt's account of the Gymnophionan brain.

[4]Weidersheim formerly thought that the double origin of the olfactory in the Gymnophiona had great morphological importance, but the studies of the Sarasins and of Burckhardt show that such is not the case.

material was none too well preserved, I am not able to say how many roots the nerve has, as it comes from the brain. Several distinct groups of fibres go from the anterior angle of the medulla to the gasserian ganglion. This latter structure is single and shows none of the double character described by von Plessin and Rabinowicz[5] in *Salamandra maculata.* Nor do my studies of the nerve fibres agree with their accounts of the nerves. The Gasserian ganglion is oval in shape. It lies in the angle formed by the otic capsule, the processes of the trabeculæ and the process ascendens of the quadrate. From its hinder surface a commissure connects it with the ganglion acustico-facialis. From its outer surface arises the maxillaris inferior, and from its anterior end, at different levels, the rami ophthalmicus superficialis, ophthalmicus profundus and maxillaris superior. The maxillaris inferior and the maxillaris superior, after leaving the ganglion, pass from the cranial cavity between the process ascendens of the quadrate and the otic capsule. According to von Plessin and Rabinowicz these rami are different in cerebral origin in *Sal. maculata,* but in my section some of the fibres which compose each are easily traced to a common origin. Of the distribution of these nerves nothing need here be said.

The two ophthalmici leave the cranial cavity through the foramen below the process ascendens of the quadrate. The ophthalmicus profundus passes beneath the optic and oculomotorius and breaks up into fibres at the posterior wall of the nasal capsule. Fibres from the ganglion of the seventh are traced through the gasserian ganglion into the ophthalmicus superficialis.

The compound facialis-auditory ganglion is long and narrow. From it arises the palatine branch which goes through

[5]According to these authors the Gasserian ganglion consists of two distinct and separate ganglia: a ventral principal ganglion and a more dorsal accessory portion. The chief ganglion has its proper medullary root, while the root of the accessory ganglion is close by and a little dorsal to the root of the acustico-facialis. From the principal ganglion arise two nerves, called respectively mandibularis (= maxillaris inferior) and nasalis (= ophthalmicus profundus); from the accessory ganglion arise the supramaxillaris superior (= maxillaris superior) and the frontalis (= ophthalmicus superficialis).

the floor of the otic capsule to be distributed as usual. The facialis branch divides into two portions just outside the cranial wall and behind and below the quadrate; the very large posterior branch runs backward to innervate the posterior belly of the digastric muscle. The anterior ramus has the usual distribution.

An especially noticeable feature in connection with the twelfth nerve is the persistence of the dorsal ganglion. Waldschmidt's observations on Protopterus and those of von Plessin and Rabinowicz upon Salamandra are interesting in this connection.

The nasal organ has a well developed organ of Jacobson, though on a simpler type than that of the Cæcilians. The sensory epithelium of the nose, is in these embryos, not differentiated as in the adult.

CONCLUSIONS.—Following such students of the Batrachia as Cope and the Sarasins it is with some diffidence that I dissent from their conclusions, for both regard Amphiuma as a connecting link between the Cæcilians and the Urodeles. That both Gymnophiona and Amphiuma are degenerate goes without question, but it seems to me that their many peculiar resemblances are those of homoplassy rather than derivations from a common ancestor. Then again, some of these resemblances have been founded upon mistakes. Thus the possession of an ethmoid by Amphiuma cannot be maintained. The external gills of the larvæ are not so similar as has been supposed; the derotrematous condition which appears later has one important difference: In Amphiuma only the third gill slit persists to open through the round external opening to the exterior, and my material shows that when the other slits were open they had separate openings upon the side of the neck. In Ichthyophis, on the other hand, the observations of the Sarasins show that both the second and third slits have a common external opening.

On the other hand, there are certain differences to be emphasized. The presence of an ethmoid in the Gymnophiona (and its absence from Amphiuma and other Urodeles[6]) the exist-

[6]The ethmoid of H. H. Wilder in Siren is clearly not homologous with the bone (mesethmoid) called by that name in other vertebrates. It is rather the prefrontal of authors.

ence of a turbinal, the absence of a parasphenoid and the presence of a basisphenoid are all points of importance, as is also the frequent presence of two rows of teeth. Again, in the Cæcilians we find a multiplicity of bones such as occurs in the lower Ichthyopsida but not in the Urodeles, and which consequently cannot be derived from the latter. Regarding the chondrocranium of the Gymnophiona no comparison can be made until the appearance of the promised paper by Burckhardt.

The view is quite common that the origin of the Batrachia (sens. lat.) must be sought in the Dipnoi. Thus Cope says (AM. NAT., xviii, p. 725–6, 1884): "The Batrachia have originated from the sub-class of fishes, the Dipnoi, though not from any known form."

This view had doubtless its foundation in the existence of both gills and lungs in these forms. As yet, however, no careful study of the distribution of the cranial nerves and of the ontogeny of the chondrocranium of any Dipnoan has been published, and until we have more detailed accounts than have as yet been made it is safe to assume that the resemblances which have been pointed out between the Dipnoi and the Urodeles are those derived from a common ancestry. Of these resemblances probably the most important is that of the relation of the mandibular arch to the skull. Thus Huxley has divided the Ichthyopsida into autostylic, hypostylic and amphistylic groups, and has shown the close resemblances of the Amphibia to the Dipnoi, Chimæroids and Marsipobranchs in the ampistylic character of this connection of the quadrate with the cranium. It is, however, to be noticed that in the Urodeles the pterygoid cartilage never has that close relation to the cranium that this thesis demands, while the autostylic condition arises comparatively late in development, and never attains that completeness which a Dipnoan ancestry would imply.

In short, I would prefer to trace the origin of both Dipnoi and Urodeles from a crossopterygian ganoid ancestry, the former being the apex of their line of development, the latter tracing their descent through the Stegocephali.

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On the Structure and Development of the Hyobranchial Skeleton and Larynx in *Xenopus* and *Pipa*; with Remarks on the Affinities of the Aglossa.

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(PLATES 8–11.)

CONTENTS.

INTRODUCTION.

CONSIDERABLE interest has for many years centred around the little suborder of the Anura Aglossa and the question of the affinities of the two sole genera, *inter se*, and with other Anura. *Pipa* and *Xenopus*, so remote from one another geographically and so essentially different in general configuration, size, dentition, spawning-habits, and many peculiarities of internal structure, yet exhibit numerous anatomical resemblances which appear to point conclusively to a common ancestry. Standing out prominently from among the latter characteristics is the remarkable complexity of the larynx and the extraordinary sexual dimorphism which it exhibits. It is with this organ that the present paper essentially deals. It both *Pipa* and *Xenopus* the relation of the larynx to the hyobranchial skeleton is so intimate, that a minute

study of the latter is necessarily demanded; and, in order to insure the correctness of the morphological value attributed to the various parts, a chapter on the development of the hyobranchial skeleton is added. I have studiously avoided all reference to the columella auris and stapedial cartilages, since these are not related anatomically with the larynx. The expression "hyobranchial skeleton," therefore, is here used in a limited and strained sense; but I do not think that any confusion is likely to be caused by this departure from the strict application of the words.

Passing over the works of Fermin (13) and Schneider (37), who mention only incidentally the hyobranchial and laryngeal skeleton of *Pipa*—*Xenopus* was not then known,—the first description of these parts occurs in a short monograph by Breyer on *Pipa* (4. 1811). Mayer (25) in his treatise on the same animal, published fourteen years later, describes for the first time the muscular system. He furnishes a detailed account of the larynx of both sexes; but the description suffers considerably from the lack of pictorial illustration. In his second contribution (26. 1835) he describes the muscles of the hyoid apparatus of *Xenopus*, and treats of the laryngeal skeleton of both sexes. To his figures of the *Xenopus* larynx (Taf. 8. figs. 6 & 7) he adds, for purposes of comparison, one of the larynx of the male *Pipa* (Taf. 8. fig. 5). By far the greater part of our present knowledge of the subject we owe to the patient and exhaustive investigations of Henle (19). Although his book refers to the vertebrate larynx generally, he has devoted quite an exceptional amount of space to the aglossal toads, and has allotted to them the whole of one of the five plates by which his work is so admirably illustrated. He describes with great care the hyobranchial skeleton of *Xenopus* and *Pipa*, the laryngeal skeleton of both sexes, and the laryngeal muscular system of the female *Pipa* and the male *Xenopus*. Henle was the first to suggest (p. 15) that the hyoglossal foramen, so characteristic of the Aglossa, is formed by a union of the anterior or hyoidean cornua, and that the hind edge of the foramen corresponds with the notch at the front of the body of the hyoid in other Anura. He agrees (p. 16) with Meckel (27. p. 229) and Mayer (26. p. 31), that the anterior cornua have been reduced in *Pipa* and are only represented by the delicate pointed cartilage at the front of the hyobranchial apparatus. Henle also (p. 16) propounded the view, already hinted at by Mayer (25. p. 541, and 26. p. 31), that the anterior

portion of the ventral wall of the larynx of both *Xenopus* and *Pipa* is in reality the hinder part of the median hyobranchial plate, and that the rod-like ossifications in the laryngeal skeleton are the columellæ or thyrohyal bones of other Anura.

The account given by Hoffmann (20) is culled almost entirely from Henle's treatise, many paragraphs being verbatim extracts. Hoffmann, however, does not seem to have had a clear idea of the nature of the coalescence of the skeletal parts described by Henle; for in two places he speaks of a fusion of the *arytenoid* cartilage with the body of the hyoid, unjustifiably substituting "cartilago-arytænoidea" in the one place (p. 518) for "Stimmladenknorpel" of Henle (p. 16), and in the other (p. 524) for "Ringförmiger Knorpel" of the same author (p. 26). Parker (33), in his exhaustive work on the skull of Batrachia, gives good figures of the hyobranchial skeleton of larval and adult stages of both *Xenopus* and *Pipa*. He ignores Henle's view of the mode of formation of the hyoglossal foramen, and by labelling the cartilage which bounds it in front the first basibranchial, tacitly suggests its origin as a secondary fenestration in the body of the hyoid. He considers the great lateral expansion of the hyobranchial skeleton of both *Xenopus* and *Pipa* as a derivative of the first and second branchial arches, and the thyrohyal as formed from the third and fourth.

Cope (7) copies Parker's figure of the hyobranchial skeleton of *Xenopus*, and gives a new interpretation to the parts, the lateral wing being considered as derived from the first, and the thyrohyal from the second branchial arch. The paper is, however, marred by contradictory statements, and the views expounded in the text do not accord with those expressed by the figure. Grönberg (18) furnishes outline text-figures of the hyobranchial skeleton of *Xenopus* and *Pipa* (p. 636), and several excellent illustrations of the larynx of both sexes of *Pipa* (Taf. 38. figs. 10–20). He pays most attention to the larynx of the male, and treats of the intrinsic laryngeal muscles of this sex alone. He regards the *whole* of the floor of the larynx of *Pipa* as derived from the branchial skeleton, and compares it (p. 635) with the cartilago thyreoidea of mammals. Wilder, in his admirable paper on the Amphibian larynx, devotes a couple of pages (42. pp. 291–292) to the hyobranchial and laryngeal skeleton of the Aglossa, and gives four figures (Taf. 21. figs. 58–61) of these structures in *Xenopus*. He refers also to the laryngeal musculature of this genus. Unfortunately his observations on the Aglossa

are not of the same standard of excellence as the rest of the work.

Such, briefly stated, is the extent of our present knowledge on the subject. With the various conflicting views and contradictory statements before me, I set myself to ascertain to what extent, if at all, the hyobranchial skeleton enters into the formation of the laryngeal box in the Aglossa; whether the lateral laryngeal ossifications of *Xenopus* are really the thyrohyals, and whether the ossifications in the floor of the larynx of *Pipa* are homologous with these. A further object of the investigation was the determination of the morphological value of the great wings of the hyobranchial skeleton in *Xenopus* and *Pipa*; the experimental verification of the assumed absence of the hyoidean cornua in *Pipa*; and an inquiry into the functional value of the great arytenoid rods which lie in the interior of the larynx in the male of this genus. The results of the investigation are arranged in the following order:—First, a comparative treatment of the adult hyobranchial skeleton of *Xenopus* and *Pipa*, including a detailed account of the laryngeal skeleton of both sexes; then a description of the laryngeal muscles of the two genera; the details of the development of the hyobranchial and laryngeal skeleton; and, in conclusion, a few observations on the bearing of the facts on the problem of the affinities of *Xenopus* and *Pipa* to one another and to the tongued Anura.

Before proceeding farther, I take the opportunity of expressing my grateful acknowledgments to Sir William Flower, K.C.B., for placing in my way every facility for the execution of this research. In addition to the adults of *Xenopus* and *Pipa*, which by the kindness of Sir William Flower I was permitted to examine at the Natural History Museum, I have received numerous specimens, both larval and adult, from Prof. G. B. Howes, of the Royal College of Science, Mr. F. E. Beddard, F.R.S., and Mr. G. A. Boulenger, F.R.S.; and to them my thanks are hereby gratefully tendered.

Hyobranchial Skeleton of *Xenopus lævis*, female.

In describing the hyobranchial and laryngeal skeleton of the Aglossa it is advisable to commence with that of the female *Xenopus*, firstly, because in *Xenopus* this portion of the skeleton is less aberrant than in *Pipa*, and, secondly, because the modification is less in the female than in the male. By choosing the

simplest of the four, we experience less difficulty in instituting a comparison with the more familiar tongued Anura; and, after having definitely settled the morphological value of each skeletal part, we can readily proceed to ascertain how the more modified parts in the other three are related to those of the first. As in other Anura, so in the Aglossa, it is impossible to draw, in the hyoid apparatus of the adult, a sharp line of demarcation between those structures which are hyoidean and those which are branchial in origin. The anterior cornua representing the main portion of the hyoid arch are present in *Xenopus*, but disappear during metamorphosis in *Pipa* (see p. 108). In both genera, however, there is a relic of hyoidean cartilage in the median cartilage situated in front of the hyoglossal foramen.

The first figure published of the hyobranchial skeleton of *Xenopus* is that of Mayer (**26.** Taf. 3. fig. 7). This is fairly correct in detail, but fails to show the hyoglossal foramen. Henle's figure (**19.** Taf. 2. fig. 1), also of the female sex, is far superior. The figure which Parker gives (**33.** Pl. 58. fig. 5) is, on the whole, less useful than Henle's. It shows that the larynx lies between the thyrohyals, but it furnishes no details of the relationship. A similar figure open to the same objection is given by Grönberg (**18.** p. 636, fig. A, ii.), and two others, with the said details introduced though incorrectly, by Wilder (**42.** Pl. 21. figs. 58 and 59).

In the female *Xenopus* the anterior or hyoidean cornu (Pl. **8.** fig. 1, *ch.*) is broad and flat, and consists of a rod-like axis, expanded on its inner and outer edges into very thin and delicate plates of cartilage which have hitherto escaped notice. At the upper posterior end of the arch the axis is unaccompanied by its lamellar expansions; it takes a sharp curve upwards and outwards, and is attached by ligament to the skull about 3 mm. from the articular head of the quadrate. At their anterior or median extremities the cartilaginous rods of the right and left cornua unite at a very obtuse angle. The external lamellæ are continuous in front of this union; but the internal or posterior expansions stop at some distance from the median line. From the point of union of the cornua there extends back a median rod of cartilage (Pl. **8.** fig. 1, *ch.'*), very slightly, if at all, broader than the axes of the cornua. The basal plate or body of the hyoid is produced outwards into two smaller anterior processes (Pl. **8.** fig. 1, *ap.*) fitting closely behind the anterior cornua, and

a pair of very large postero-lateral plates, usually described as the "alæ" or "wings" (Pl. 8. fig. 1, *a*)—a most convenient term, as it merely designates the part without expressing its morphological value. The true value of these processes is discussed later, chiefly upon the evidence furnished by a study of the development. The alæ are perfectly flat plates of cartilage, with an even margin, slightly pointed posteriorly, and with a blunt notch on the mesial edge at about one-fourth of the length from the posterior extremity. The greatest diameter, at about one-third from the posterior end, is rather more than one-third of the length. Mayer (26. p. 33) says that in the female *Xenopus* the wings are smaller and thinner than in the male, a statement with which I cannot agree. But since he says (p. 29) the male "ist grösser und schlanker gebaut als das Weibchen," it is evident that his female specimens were not up to the average size, or that his males were exceptionally large. The anterior processes and the alæ are of the same thickness of cartilage as the basal plate itself; but there is a much thinner extension of cartilage, recalling the lamellar expansions of the anterior cornua, which forms the lateral margin. This thins away behind along the external margin of the ala, and is continued forward around the external and anterior edge of the anterior process. It is indicated in Plate 8. fig. 1 by fainter shading.

The hyoglossal foramen (Pl. 8. fig. 1, *h*), which is such a conspicuous feature of the hyobranchial apparatus, is mainly closed by membrane: the hyoglossal muscles, which rise up to be distributed to the mucous membrane of the floor of the mouth, pass between the posterior edge of the membrane and the cartilage which bounds the foramen posteriorly (Pl. 8. fig. 1, *y*). The shape of the fontanelle varies; but it is always oval and elongated in an antero-posterior direction, its greatest diameter lying behind the middle of its length. Henle (19. p. 15), with remarkable introspection, considered that the hinder border of this hole in the basal plate represents the anterior edge of the basal plate of the hyobranchial skeleton of the frog, and that the presence of the foramen is to be explained by the union of the two anterior cornua in front. He based his conclusions almost entirely on the relations of the hyoglossal muscles; but, as I hope to prove in the sequel, he was fully justified in his determination. Behind the foramen the basal plate is sharply constricted, but it almost immediately widens out behind, and becomes indistinguishably

fused with the anterior edge of the cricoid cartilage of the floor or ventral wall of the larynx, in the position marked *x* in fig. 1. The reasons for fixing this as the region of coalescence are based upon a comparison of the cricoid skeleton with that of the frog (see p. 62) and on a study of the development of the parts (see p. 100). The distance *yx*, therefore, in fig. 1 represents the very greatly diminished antero-posterior diameter of the large basal plate of the frog's hyobranchial skeleton. Henle has already pointed out in the middle of the basal cartilage of *Xenopus* an incipient ossification, which he compares (19. p. 17 footnote) with that larger V-shaped ossification which occurs in the middle of the body of the hyoid of *Alytes*. The ossification occurs only late in life, so that it is quite possible for the larynx of a sexually mature *Xenopus* to show no trace of it.

Externally to the region of coalescence between the laryngeal cartilage and the basal plate, and separated from it by two small membranous areas, are the anterior ends of two rods of bone which project backwards and, diverging slightly, run along the right and left sides of the larynx proper (Pl. 8. fig. 1, *t*). These rods are circular in section, are thicker behind than in front, and are narrowest at a short distance from the anterior end. The posterior epiphyses are cartilaginous and exhibit, in fully grown specimens, an incipient endochondral ossification (Pl. 8. fig. 3, *ep.*). The epiphysis is fused mesially with the hind end of the lateral walls of the cricoid cartilage. The rods are the only fully ossified parts of the whole hyobranchial and laryngeal skeleton; and in this respect, as also in form, they resemble the columellæ or thyrohyals of the tongued Anura *, with which they have been considered homologous by all writers who have given attention to the subject, from Henle onwards. The attachment of the rods to the hind part of the basal plate, their lateral position with regard to the larynx proper, their divergence even, all point to the same conclusion; and, since I hope to prove in the following pages that all the salient features of the cricoid and arytenoid cartilages of the larynx of the frog or other anuran can be distinctly recognized in the cartilaginous apparatus that lies between the two bony rods in the female *Xenopus*, there would appear to be here sufficient evidence, without having recourse to that afforded in addition by a study of the relations of the muscles,

* Ossifications in the body or basal plate occur in *Bombinator*, *Alytes*, and other forms; but even in these the columellæ are the most completely ossified.

and of the development of the rods themselves, to firmly establish the homology. The posterior ends of the thyrohyals are wider apart than the inner edges of the alæ, and lie below or ventral to the latter. The posterior epiphysial cartilages are bound by a very short and tough ligament to the ventral surface of the alæ, just external and slightly posterior to the notch on their inner edge already mentioned.

Laryngeal Skeleton of *Xenopus lævis*.

The first account of the larynx of *Xenopus* is that of Mayer (26. 1835). He describes both sexes and gives figures of each (Taf. 3. figs. 6 and 7). Henle (19), like Mayer, discusses both sexes, and his figures of the dorsal and ventral surfaces of the female larynx (Taf. 2. figs. 1 and 2) are exceedingly accurate. The larynx described by Wilder (41. p. 573, and 42. pp. 291 and 292) must have been in a sad state indeed if his figures (42. Taf. 21. figs. 58–61) represent it at all truthfully. These show a number of dismembered cartilages in the roof, and no cartilage in the floor. It is, also, hardly just and fair to condemn Henle's excellent work and to charge him with overlooking the true arytenoids, on the strength of observations made, as Wilder himself admits (42. p. 290), on a single specimen. This most recent contribution of Wilder's is so good in the main that it is a great pity it has been marred by the incorporation of the results of "hasty study."

Female.

The larynx proper of *Xenopus* differs from that of the more normal anuran, not only in its superior size and the extensive spreading of the cricoid cartilage so as to form an almost complete laryngeal box, but more especially in the union of the lateral edges of its floor with the inner surfaces of the ossified thyrohyals, the confluence of the anterior region of the floor with the back of the basal plate of the hyoid, and in the coalescence which has taken place between the posterior epiphysis of the thyrohyal and the postero-lateral corners of the cricoid. Although the lateral edges of the floor of the larynx are so closely applied to the columellæ, the actual sides of the larynx are free, and the narrow space between them and the thyrohyals is filled with a fatty tissue similar to that found on the under surface of various parts of the hyobranchial skeleton. There is a pear-shaped membranous area (Pl. 8. fig. 2, *f*) in the cartila-

ginous side-wall of the larynx, which is of considerable value as a guide to the recognition of homologous parts in *Xenopus* and *Rana* (see p. 62). The floor or ventral wall of the larynx has the form of an extensive plate of cartilage, incomplete only in a pair of elongated membranous areas (Pl. 8. fig. 1, *f'*) towards its anterior end, where the anterior fifth of the thyrohyal remains free.

The floor of the larynx is produced posteriorly into a pair of cartilaginous bands (*br.*) with very irregular edges, which run back along the mesial surface of the bronchi, in the possession of which latter the Aglossa depart again from the anuran type. The irregular outgrowths from the sides of the bands extend only to the middle of the upper and under surfaces of each bronchus, so that the outer half of the bronchial tube is entirely membranous. These bronchial prolongations of the cricoid cartilage are not unrepresented in other Anura, for in the Discoglossidæ (e. g. *Discoglossus*) two thin cartilaginous bars run back from the floor of the larynx to the under surface of the root of the lung, where they end in a cross-piece, T-shaped, which may be regarded as equivalent to one of the bronchial half-rings of *Xenopus*. In *Alytes* these rods are even more elongated than in *Discoglossus*, but the terminal T-piece is very little developed. In *Bombinator* the processes are quite short and stout (Pl. 11. fig. 13, *br.*). Even in *Rana* the opening of the lung into the larynx is supported by a ring of cartilage which sends off irregular processes on to the lung. The strongest of these (Pl. 9. fig. 7, *br.*), running along the ventro-internal aspect of the lung, would appear to correspond with the process already referred to in the Discoglossidæ, and with the bronchial cartilaginous band of *Xenopus*. The roof of the larynx of the female *Xenopus* is deeply notched behind (Pl. 8. fig. 3), so that a membranous area intervenes between the cricoid and bronchial cartilages. The anterior edge of the roofing cartilage is delicately rounded, and is rather thicker than the other parts. The antero-posterior diameter of the roof is not more than twice the transverse diameter.

The arytenoid, like the cricoid, is exceptionally shaped. The sides of the glottis are supported by a pair of delicate cartilaginous flaps (Pl. 8. fig. 3, *ar.*) which, from their relations to the glottis and to the laryngeal muscles, evidently correspond to the arytenoid cartilages as we find them in the common frog. They are continued backwards into relatively massive processes (*ar.'*)

which, behind the glottis, meet one another in the median plane by perfectly flat and smooth articular surfaces *. These masses of cartilage lie immediately in front of the thickened anterior edge of the roofing cartilage of the larynx and usually contain a small centre of ossification each. These ossifications, like those of the posterior epiphyses of the thyrohyals and the anterior part of the floor of the laryngeal complex, only appear with advancing age. A female may be fully grown and sexually mature without exhibiting a trace of ossification in these regions. The lateral motion of the arytenoids is limited by a pair of concavo-convex upgrowths of the side-walls of the larynx (Pl. 8. fig. 3, *bl.*), called by Henle (p. 17) the "Scheuklappenartige Fortsätze" or blinker-shaped processes. There are no vocal cords, and their absence may account for the exceptional shape and mutual relations of the arytenoids. The failure of the arytenoids to touch one another in front of the glottis is also a matter of no little importance.

The relations that obtain between the cricoid cartilage of *Xenopus* and that of other Anura can best be made out by the study of a median section of the laryngeal skeleton. By this means it is seen that the roofing part of the larynx of *Xenopus* (Pl. 8. fig. 2, *c*) is nothing more than the median dorsal rod, greatly expanded, of *Rana esculenta* (Pl. 9. fig. 7, *c*), while the floor (Pl. 8. fig. 2, *c′c″*) is made up of the coalesced enlarged transverse bars (Pl. 9. fig. 7, *c′* & *c″*). Even the blinker-shaped processes of *Xenopus* (Pl. 8. fig. 3, *bl.*) can be recognized in the frog's larynx in the swellings (Pl. 9. fig. 7, *bl.*) at the sides of the anterior ventral bar of the cricoid. The membranous area (Pl. 8. fig. 2, *f*) in the side-wall of the larynx of *Xenopus* is a great guide in the determination of the parts, since it fixes the position of the space (Pl. 9. fig. 7, *f*) at the sides of the ring of cartilage on the ventral surface of the frog's larynx. Owing to the great expanse of cricoid cartilage in *Xenopus*, the connexion with the posterior epiphysis of the thyrohyal, situated in the frog close behind the arytenoid (Pl. 9. fig. 7, *l′*), is thrown

* Seeing that in the larval larynx (Pl. 11. fig. 10) the arytenoids are in contact with the anterior edge of the dorsal part of the cricoid, and are even overlapped by it, it becomes doubtful whether, after all, the massive part of the arytenoid of the adult is a *process* of the true arytenoid—it may be simply an *enlargement* of the posterior end. In the male of *Pipa* it is tolerably certain that the bulk of what is known as the arytenoid is really a process of the true arytenoid; but the relations are simpler in *Xenopus*.

very far back (see Pl. 8. fig. 8), and the union is brought about in *Xenopus* by the confluence of the cartilages and not by ligament as in the frog. Henle states (p. 14) that in *Alytes obstetricans*, *Bufo cinereus*, *Rana esculenta*, and *Rana temporaria* the larynx is connected with the epiphysis of the thyrohyal by continuous cartilage. I have examined these four species, and have found the connexion to be ligamentous in all. Wilder refers (42. p. 286) to a cartilaginous union in *Bufo lentiginosus*, but the difficulty of obtaining this species in England has prevented me from checking the observation. Relatively to the size of the whole body, the arytenoids are much smaller in *Xenopus* than in the frog, although the larynx as a whole is very much larger. I have elected to institute this comparison with the larynx of the edible frog, not merely because the figures of the latter by Ecker (12) and others are so familiar to the majority of anatomists, but also because of the fact that the laryngeal skeleton of the female *Xenopus* will bear a closer comparison with that of *Rana esculenta* than with that of any other species of *Rana*. It is true that Wilder (42. p. 287) has shown that the larynx of *Rana esculenta* is not typical of Anura, nor even of the genus *Rana*; but by the very possession of the posterior ventral bar of the cricoid (Pl. 9. fig. 7, *c''*), in which it departs from the other species of the genus, the larynx of the edible frog approaches the nearer to that of *Xenopus*.

In spite of this parallelism existing between the larynx of *Xenopus* and that of the frog, an extensive study of the skeleton of many different genera of Anura has convinced me that that amphibian (*Pipa* excepted) the hyobranchial and laryngeal skeleton of which most nearly approximates to that of *Xenopus* is undoubtedly *Bombinator*—a determination which I had arrived at prior to the publication of the hint to the same effect by Wilder (42. p. 291). The notch at the front of the hyobranchial basal plate in this toad is excessive, so great in fact as to leave only a narrow transverse isthmus connecting the right and left halves, as in some Hylidæ *. The paired ossifications in the

* In spite of the depth of the notch at the front of the basal plate, the point at which the hyoglossal muscles rise above its level is not in any way thrown back. The notch is closed by a membrane, the front edge of which lies nearly straight and is situated a considerable distance in front of the incised cartilage. This holds good also for *Alytes*, *Discoglossus*, *Rana*, *Bufo*, and most Anura where the notch is at all deep. In *Xenopus* the hyoglossal muscles rise immediately in front of the cartilage that forms the posterior border of the oval foramen, while the membrane spreads out in front over the rest of the hole.

body of the hyoid of *Bombinator* are exceptional, and these are not represented in *Xenopus*; but the large size of the lateral processes of the hyobranchial skeleton, more especially the posterior pair, is significant, and the great breadth of the plate-like hyoidean cornua renders them remarkably similar to those of *Xenopus*. The laryngeal skeleton of *Bombinator* is not only expansive and dome-shaped, and larger in the male than in the female, but is also elongated in an antero-posterior direction, especially in the male sex. These features are well illustrated by Wilder (42. Taf. 21. figs. 45–47), but in his figures he unfortunately omits the conspicuous bronchial processes that project from the posterior edge of the cricoid cartilage (Pl. 11. fig. 18, *br.*). The broadening of the cricoid cartilage in *Bombinator* is, as in *Discoglossus* (where, owing to the larger size of the larynx, the fact can be better made out), confined to the roof and floor. The sides consist of mere bands or rods of cartilage extending vertically from roof to floor, and the ligament that runs out to the thyrohyal epiphysis is attached to the middle of the external surface of the bar.

In the Discoglossidæ, as in the Aglossa, there are no traces of what Henle (p. 11) calls the cartilages of Santorini, small abstricted portions of the arytenoid cartilages occurring in a limited number of Anura, and first figured by Saint-Ange (36. Pl. 26. figs. 4 & 5). They are the "pre-arytenoid" cartilages of Ecker (12) and the "apical" cartilages of Wilder (42). The absence of these cartilages, however, cannot be allowed to carry much weight, since they are not constant in closely allied genera, and may even be sometimes missing in the female of a species normally possessing them (12. p. 313).

Male.

The sexual differences in the laryngeal skeleton, so striking in the aglossal Anura, are nevertheless not confined to them. Wilder (42) has already pointed out that in *Bufo* there are suggestions of sexual dimorphism in the larynx, and that important sexual differences occur in the Hylidæ and in *Bombinator*. But the increased size and complexity of the larynx in the male is even more widely spread among Anura than he indicates. Ecker (12. p. 313) has shown that in *Rana esculenta* the arytenoid cartilages are thick, strong and large in the male, and thin, smaller and more hollowed in the female. In *Alytes* and

Discoglossus I find that the sexual differences are quite as strongly marked as in *Bombinator*, while in *Pelobates*, *Ceratophrys*, and *Pelodytes*, although the differences are less pronounced, they are clearly recognizable. It is highly probable that more extended observations will amplify the list still further.

In the male *Xenopus* the larynx, relatively to the size of the hyobranchial skeleton and to that of the whole body, is considerably greater than in the female, but yet, owing to the smaller size of the male as compared with the female, the actual cubic content of the larynx is about the same in both. The larynx of an average male is shorter than that of the average female, but it is broader and more inflated. The roof, also, extends proportionately farther forward. The narrow bar of cartilage (Pl. 8. figs. 1 and 3, *x*), which forms the hinder edge of the hyoglossal foramen in the female, is in the male partially replaced by ligament (Pl. 8. figs. 4, 5, and 6, *l*). This is a matter of the highest importance from a morphological point of view, for the substitution has the effect of severing the true basal plate of the hyobranchial skeleton from its lateral outgrowths in such a way as to make it appear part of the laryngeal skeleton. The basal plate, already so reduced in size, is now separated from all the rest of the hyobranchial skeleton, except the thyrohyals. In it Henle (19. p. 17) has described a hexagonal ossified plate, evidently a further development of the small centre of ossification occurring in the same position in the female. I must confess that in the specimens which I have had the opportunity of examining I have found no trace of ossification in this region. Whether my specimens were too young, or whether Henle's specimen was abnormal I cannot say,—the bony plate which he figures is so large in comparison with the remainder of the larynx that it is hardly likely that his observation is at fault.

The thyrohyals are slightly curved, although straight in the female; and, owing to the lateral expansion of the laryngeal skeleton proper, they appear to lie more on the ventral side of the larynx than in the female (see Pl. 8. figs. 1, 3, 4 and 6). It thus happens that they are not visible in a dorsal view of the skeleton, whereas in the female very little of the thyrohyal is overlapped by the cricoid cartilage (see Pl. 8. fig. 3). The floor of the

larynx of the male is complete *, the membranous spaces which occur between the anterior ends of the thyrohyals in the female being filled up by cartilage. The portion of the side-wall of the larynx situated externally to the arytenoids is much more massive in the male; and, whereas in the female the blinker-shaped process terminates anteriorly in an abrupt edge, it fuses in the male with the true basal plate of the hyobranchial skeleton (Pl. 8. fig. 6, *bl.*). The cricoid cartilage is very much thicker than in the female, and the thickening has proceeded irregularly into the interior of the larynx (Pl. 8. fig. 5) in a manner recalling the formation of the turbinal ingrowths of the nasal capsule in higher vertebrates. The general impression is one of solidity and massiveness, in striking contrast with the delicacy and elegance of the female larynx.

A comparison of median sections of the male and female larynx (Pl. 8. figs. 5 and 2) shows that most of the differences are those of degree and not of kind; but there is one most important structural dissimilarity to be noted. The posterior processes of the arytenoid cartilages of the male are confluent with one another (Pl. 8. fig. 6, *ar.'*). The union is brought about by a thin horizontal sheet of cartilage, situated immediately behind the glottis, and dorsal to the broad, flat, articular surfaces by which, as in the female, the two massive parts are applied to one another in the median plane (see fig. 5). The relations of the connecting cartilage are such as to warrant the assumption that there is here a procricoid cartilage, not free as in the female *Pipa* (Pl. 9. figs. 2 and 3, *pc.*), but united on either side with the arytenoids. This is certainly the most plausible explanation of the facts, but it involves the curious anomaly, that a procricoid cartilage is present in the male *Xenopus* and in the female *Pipa*, while no trace of it can be detected in the female *Xenopus* and in the male *Pipa*. The arytenoids proper (Pl. 8. figs. 5 and 6, *ar.*) stand nearly vertically, and do not slope downwards and outwards as in the female. Henle (p. 18) states that the arytenoids are ossified in the male, but this I am not in a position to confirm.

The bronchial cartilages are disposed just as in the female. The bronchi have long been known to be shorter in the male than in the female, but undue stress seems to have been laid on this fact in consequence of the failure to take into account the

* Wilder erroneously states it to be entirely membranous (**42**. p. 292, and Taf. 21. fig. 59).

smaller size of the body of the male. An extensive series of measurements shows that the proportion between the length of bronchus and the distance between the snout and cloaca is the same—one-seventh—in both sexes.

Hyobranchial Skeleton of *Pipa americana*, Female.

The first figures published of the hyobranchial skeleton of *Pipa* are those of Breyer (4). These figures, correct as far as they go, show, however, none of the details of the skeletal parts lying towards the median line. Mayer (25), in his monograph on *Pipa*, says very little about the hyobranchial skeleton, and gives no figures of it. It is in his paper on *Xenopus* (26. p. 31) that he mentions the absence in *Pipa* of the anterior or hyoidean cornua—a fact previously noticed by Meckel (27. p. 229). Henle's description and figure (19. Taf. 2. fig. 11) of the female are the first upon which any reliance can be placed. Henle agrees with Meckel and Mayer that the anterior cornua are reduced, and states (p. 16) that they are only represented by the pointed cartilage at the front of the hyobranchial skeleton. Parker (33. p. 651) was the first to show that the hyoidean cornua are present in the embryo. He does not figure the hyobranchial skeleton of the adult, but in the ripe young, just about to quit the maternal pouches (Pl. 60. fig. 7), this portion of the skeleton has already acquired most of the characters of the adult. A criticism of this figure will be found on page 110. The figure furnished by Grönberg (18. p. 636, fig. A. iii.), although only an outline text-figure, shows more accurately than any published previously the relations obtaining between the hyobranchial and the laryngeal skeleton in the female.

On comparing the hyobranchial skeleton of the female *Pipa* with that of *Xenopus*, one recognizes at once the large wings (Pl. 9. fig. 1, *a*), the greatly reduced basal plate (*yx.*), and in front of it the large foramen (*h*) through which the hyoglossal muscles rise to be distributed to the mucous membrane of the floor of the tongueless mouth. The basal plate and the thyrohyals (*t*) have entered into the formation of the floor of the larynx; the bronchi are elongated and are supported by bronchial cartilages (*br.*). The hyobranchial skeleton terminates in front in a tapering rod of cartilage (*ch.'*), evidently the homologue of the rod-like cartilage (Pl. 8. fig. 1. *ch.'*) which extends forwards in front of the hyoglossal foramen in *Xenopus*. The foramen is

more circular in *Pipa* than in *Xenopus*, but tends to become elliptical with increasing age. Even in very old specimens the antero-posterior diameter is not vastly in excess of the transverse, so that the hole is never so drawn out as in the middle-aged *Xenopus*. As in this latter genus, the anterior three-fourths of the foramen are closed by a fatty membranous tissue.

The antero-lateral processes of *Xenopus* (Pl. 8. fig. 1, *ap.*) are missing, and the wings are of an entirely different shape. The stalk of attachment to the axial parts of the hyobranchial skeleton is very narrow. The basal plate is much constricted a short distance behind the hyoglossal foramen so as to be divided into two parts connected by an isthmus (Pl. 9. fig. 1, *i*). The anterior portion forms the hinder border of the foramen, the posterior enters into the constitution of the floor of the larynx. It is from the posterior edge of the latter portion that the thyrohyals arise. Henle states (19. p. 16) that the isthmus is ligamentous as it is in the male; but Grönberg (18. p. 635) has already corrected this error. The hyobranchial skeleton of the old female differs in numerous particulars from that of the female just sexually mature. The foramen, as already pointed out, is elliptical instead of circular, the pointed cartilage in front is longer and thinner, the wings are more incised on their inner margin, while the stalks are narrower and more elongated. Breyer states (4. p. 14) that the "lamina" or wing of the hyobranchial skeleton of *Pipa* is longer and narrower in the male than in the female. Meckel (28. Theil iv. p. 338) agrees with Breyer that the wing of the female *Pipa* is broader than that of the male, but says it is longer also. Mayer (26. p. 32) affirms that the wing is especially broad and strong in the male. The difference in proportion is, however, in my opinion, one of age, not of sex.

Laryngeal Skeleton of *Pipa americana*.

The first mention of the larynx of *Pipa* was made in 1764, by Fermin, who describes it in the male as the lambdoid bone *;

* Fermin, 13. p. 150. "* * * deux cavités distinctes et séparées l'une de l'autre par un diaphragme, attaché à un Os triangulaire, qui a la forme d'un Ω grec, que l'on pourroit appeler l'os *Lambdoïde*. Il est situé au dedans de la cavité générale, ou sa base se trouve fixée par un fort ligament à la partie supérieure du *Sternum*; et duquel il déborde un peu. De la base du même Os sortent deux ligamens assez forts qui s'implantent dans la partie moyenne de la machoire inférieure."

and the first figures are those of Schneider (37. Tab. 2. figs. 4, 7–11). The specimen figured, a male, was in a bad state of preservation, and this it was in all probability which led Schneider into the mistake of regarding the larynx as a constituent of the sternal skeleton (37. pp. 261 and 263). The larynx of *Pipa* was first described in any detail by Breyer (4), who gives figures, rather poor, of both sexes. A much better description, referring principally to the male larynx, was furnished in 1825 by Mayer (25), but without figures. In his paper on *Xenopus*, ten years later, he gives a figure (26. Taf. 3. fig. 5) of the larynx of the male *Pipa*, broken open to show the elongated arytenoids lying within. The first figures showing the detailed structure of the larynx we owe therefore to Schneider and Mayer, and not to Henle as stated by Grönberg (18. p. 634), who appears not to have seen the 'Historia amphibiorum' nor Mayer's second contribution. Much valuable information is to be gathered from Henle's careful description and illustrations of the larynx of both sexes. The study of the larynx of *Pipa* was again undertaken by Grönberg in 1894, and the eight figures that he gives (18. Taf. 38. figs. 10–17) are excellent. He treats of both sexes, but chiefly of the male.

Female.

The larynx of the female *Pipa* is smaller in proportion to the size of the whole hyobranchial skeleton than in the *Xenopus* female. It is also relatively shorter in an antero-posterior direction, but the length increases with age. The only ossified parts are the thyrohyals (Pl. 9. fig. 1, *t*), which are very much shorter, broader, and flatter than in *Xenopus*, and are situated in the floor of the larynx and not at the sides. Their anterior ends are nearly in contact, and the posterior epiphyses are indistinguishably fused with the postero-ventral band of the cricoid cartilage. The space between the bones themselves is closed by membrane, a fact which Grönberg in his excellent paper fails to notice, although Meckel (28. Theil vi. p. 451) and Henle (19. p. 19, and Taf. 2. fig. 11. *.) had already pointed it out. Breyer states that the ossified bars are absent in the young female. His figure (4. Tab. 2. fig. 5) of the adult female larynx he subscribes "Larynx femina a parte inferiore cum laminis osseis," but he most unfortunately locates the bones on the roof of the larynx in his text (p. 15), "lamina inferior mere cartilaginea est;

lamina superior pariter cartilaginea duo tamen exhibet ossicula plana," etc. This error was exposed by Meckel in 1833 (28. Theil vi. p. 451). It may be well to point out here that, while Henle describes the orientation of parts with the toad standing on its hind legs in an erect, human position, Breyer and most writers place the animal belly downwards. What, therefore, in this paper is called the roof of the larynx, is the 'lamina superior' of Breyer, the 'dorsale Wand' of Grönberg, and the 'hintere Wand' of Henle. Wilder (42) avoids the difficulty by speaking of the 'pharyngeal' and 'cardiac' surfaces.

The roofing cartilage of the larynx has a deep angular notch posteriorly and an approximately semicircular one anteriorly. The incisions are so deep that a median longitudinal section of the larynx shows only a very small extent of cartilage in the roof (Pl. 9. fig. 3, *c*). Into the anterior space there fits a thin unpaired plate of cartilage, which overlaps the hinder portions of the arytenoids. This plate (figs. 2 and 3, *pc.*) is probably to be regarded as a dismembered part of the cricoid cartilage. Its nearest representative, Henle points out (19. p. 43), is the small cartilage similarly placed in some Chelonia, (see Henle, 19. Taf. 5. figs. 28 and 29, *d*). Dubois (9. p. 181, and fig. 5) calls this latter the procricoid, and the name may safely be extended to the cartilage under consideration in *Pipa*.

The arytenoid cartilages are rather larger in proportion to the size of the larynx than in the female *Xenopus*, and the process (Pl. 9. figs. 1 and 2, *d*) to which the tendon of the dilator muscle is attached extends outwards considerably beyond the outer margin of the thyrohyal; whereas in *Xenopus* the whole of the arytenoid is confined to the space between the two thyrohyals (*cf.* Pl. 9. figs. 1 and 2, and Pl. 8. fig. 3). The anterior parts supporting the sides of the glottis are thin; the posterior parts underlying the procricoid, although touching one another in the median line, are not massive as they are in *Xenopus*, nor do they articulate by broad flat surfaces. A median section of the larynx shows the existence of a firm fibrous mass (fig. 3, *vc.*) covered by a thin mucous membrane, and attached to the mesial surface of the arytenoid cartilage. Its posterior edge is free, and although the tissue is not as elastic as the vocal cord of tongued Anura, there can be little doubt that the two structures are homologous. It may be said of the male *Pipa* and of both sexes of *Xenopus*, that vocal cords are absent, but this statement should be

qualified in respect of the female *Pipa*. The median section also demonstrates the small extent of cartilage in the median line of the roof (fig. 3, *c*) and floor (*c″*) of the larynx. Owing to the close approximation of the anterior ends of the thyrohyals and the presence of the membranous space in the floor of the larynx there is less difficulty than in *Xenopus* in recognizing the morphological posterior edge of the basal plate of the hyobranchial skeleton (figs. 1 and 3, *x*). The fenestra seen in the side-wall of the larynx of *Xenopus* does not occur in *Pipa*.

The bronchi are elongated and are supported by bronchial cartilages. These cartilages have the form of independent bronchial rings, and are not, as they are in *Xenopus*, united into a band running lengthwise along the bronchus. The bronchial skeleton is also more complete in *Pipa*, the rings extending three quarters of the way round, while in *Xenopus* the lateral projections of the longitudinal bronchial cartilage do not extend more than halfway round. And, what is still more important, the bronchial rings of *Pipa* are incomplete on the mesial side, whereas in *Xenopus* it is the external wall of the bronchus that is not supported by cartilage.

Male.

The larynx of the male *Pipa* is unique and unparalleled not only among the Anura but in the whole animal kingdom. It is almost entirely ossified, and thus contrasts forcibly with the larynx of the male *Xenopus* which, although more massive and inflated than that of the female, is certainly not more bony. The larynx of the male *Pipa* is about twice as long as that of the female—five or six times so according to Mayer (25. p. 540), but this computation is excessive. It is proportionately broader in front, so that in a dorsal or ventral view it has roughly the form of a rectangular cushion or pillow. The floor is continued forwards into a pointed process of unossified cartilage, which is attached by ligament (Pl. 9. fig. 5, *i′*) to the middle of the transverse bar forming the posterior boundary of the hyoglossal foramen. The cartilaginous process at the front of the larynx and the bar bounding the back of the foramen are the posterior and anterior portions respectively of the basal plate of the hyobranchial skeleton. The ligament connecting them has the same morphological value as the cartilaginous isthmus of the female (Pl. 9. fig. 1, *i*). It must not be confounded with the paired

ligament (Pl. 8. fig. 6, *l*) of the larynx of the male *Xenopus*, although the physiological significance is probably the same. The ligament in *Pipa* connects the anterior and posterior portions of the basal plate, but in *Xenopus* the basal plate is not subdivided, but is incorporated bodily into the constitution of the larynx, while the ligaments arise from its anterior end. Except in the ligamentous nature of the isthmus the hyobranchial skeleton of the male *Pipa* does not differ materially from that of the female.

The laryngeal walls are remarkably complete; the roof (Pl. 9. fig. 4) extends nearly as far forwards as the floor, and the notch in its posterior border is but slight. The floor has a small but deep notch behind (Pl. 9. fig. 5) and, a short distance in front of the notch, a pair of small fenestræ; but beyond these it is one expanse of bone. The greater part of the floor is formed by the flattened thyrohyals, which can be distinguished from the rest of the bone by their yellower colour and closer texture. The two thyrohyals actually touch one another anteriorly, and the membranous area in the floor of the female larynx is here closed by a narrow strip of ossified cartilage. Along the sides of the larynx the junction of the cricoid and thyrohyal is marked by a very conspicuous groove (fig. 6). The roof of the larynx is marked by a cruciform area in which the ossification is less complete than elsewhere. Grönberg (18. Taf. 38. fig. 11) represents this in his figure as actually cartilaginous.

Although Grönberg was unable to consult Henle's treatise on the larynx, and had to remain content with the copies of the figures of that work published in Bronn's 'Klassen und Ordnungen' (20), he detected that Henle had confounded the dorsal and ventral surfaces of the larynx of the male *Pipa*. Curiously enough, Henle (19. p. 20 footnote) charges Breyer with doing exactly the same thing. "Rudolphi hat die hintere und vordere Fläche verwechselt." As a matter of fact, Breyer's description is correct and Henle himself was wrong. He had probably observed that Breyer had described the thyrohyals on the wrong surface of the female larynx, and became afterwards confused as to the sex for which the description was erroneous.

The two bronchi open together close to the median plane, by a pair of apertures which occupy only a small proportion of the posterior laryngeal wall. The bronchial cartilages are arranged as in the female. The bronchi of *Pipa* have since the

time of Breyer (4. p. 15) been known to be longer in the female than in the male, but the difference seems to have been much exaggerated. Grönberg (18. p. 638) puts the length of bronchus of the male at 15 to 20 mm., and that of the female at 25 mm., and my own measurements accord tolerably well with these.

The arytenoids are even more remarkable than the rest of the laryngeal skeleton. The glottis, which is small in proportion, is situated quite at the front of the pillow-shaped larynx. It is bounded by small arytenoid cartilages (Pl. 9. fig. 5, *ar.*) which are continued outwards and backwards as relatively huge bones (*ar.'*), each provided with four articular surfaces and two processes for muscle-attachment. The bulk of each bony mass has the form of a rod with a very irregular warty surface. The rods extend the full length of the laryngeal cavity: their posterior ends are bluntly pointed and lie over the bronchial apertures. They are composed of a very hard and brittle bone, and when broken across exhibit a central whiter and softer part. Their extreme length is about 22 or 23 millim. What renders these rods the more remarkable is the fact that there is not the least suggestion, anticipation, or foreshadowing of them in the female. The posterior parts of the arytenoids of the female *Pipa* are insignificant even when compared with those of the female *Xenopus*. Henle has already figured and described * with great minuteness the configuration of these bones, so that it will here suffice to state that they articulate with one another by two pairs of processes, one towards the dorsal and the other towards the ventral side, and that each articulates by a large flat surface with the roof (figs. 4 and 5, *v*), and by a ball-and-socket joint with the floor of the larynx. As a consequence of these peculiarities of articulation the rods lie close up to the roof, and are raised somewhat above the floor. The fibrous tissue which occupies the position of the vocal cords is less conspicuous than in the female, but the arytenoid cartilages are distinctly hollowed out, and are thickened along those edges that bound the glottis. Although there is a very sharp line of demarcation between the cartilage and bone, the two are perfectly continuous and move

* In referring to Henle's description it must not be forgotten that he had confounded the dorsal and ventral surfaces, and that in his figures (19. Taf. 2. figs. 16–20) the words 'vorn' and 'hinten' must be transposed throughout. In Mayer's earlier work (25. p. 541), where a less detailed description is given, the orientation of parts is correct.

together. I fail to see what advantage is to be gained by giving distinct names to the cartilaginous and ossified portions as Grönberg does (18. p. 636).

The hinging of the rods is such that they can swing in the horizontal plane, and the free posterior ends are capable of moving through a distance of about 3·5 millim. each. The hinder parts of the rods can touch one another in the median plane, as may be seen by manipulation, and more conclusively by the flatness of the more projecting parts of their mesial surfaces, where the impact, of which more anon, normally takes place. They are, however, prevented from crossing the middle line by a forwardly directed process of cartilage (Pl. 9. fig. 5, *cr.*) standing up from the inner surface of the posterior part of the floor of the larynx. A similar crest, of much smaller size, hangs down from the roof. The two rods are notched internally, so that they can strike one another without encountering these crests. The rods are actuated by special dilator muscles attached to outstanding processes (Pl. 9. fig. 5, *d*) of the parts situated anteriorly to the centre of oscillation (*v*). On the contraction of the muscles the anterior parts of the rods are divaricated, and the longer posterior portions are brought into contact.

Although Müller (30. p. 222) has compared the rods with the two prongs of a tuning-fork, most authorities liken them to the clapper of a bell. Mayer, for instance, states (25. p. 542) that they are disposed in such a manner, "dass sie an die innere Wandung der Höhle desselben, wie der Schwengel in der Glocke, anschlagen können." Henle erroneously regarded the bones as fixed in position and unable to swing bodily to and fro, and concluded (19. p. 31) that the sound uttered must be due to molecular vibration. Grönberg (18. p. 637) exposed the fallacy of this statement and showed that, although the rods do not swing about fortuitously at every movement of the animal, they are nevertheless capable of motion, and that they are controlled by special muscles attached to them. A study of the muscular mechanism has convinced me that the rods do not beat against the laryngeal walls as a clapper strikes a bell, but that they strike one another in the manner indicated above. It is evident that the larynx is thus curiously modified for the production of sound, and the sound to be expected on *a priori* reasoning is a series of short, sharp taps caused by the impact of the rods, following one another as quickly as successive contractions of

the muscles can be effected,—a sound similar to, though probably more rapidly repeated than, the taps given by certain wood-boring beetles.

Having arrived at this conclusion, it was most gratifying to me to hear Mr. Arthur Thompson, when recounting at a recent meeting of the Zoological Society his observations on the habits of the Surinam toads then breeding in the Society's menagerie, mention, quite incidentally, the rapping noise which they made. All those anatomists who have paid any attention to the subject have remarked on the failure of anyone to hear the sound, which they were convinced must emanate from such a complicated laryngeal apparatus. Grönberg, in his recent contribution, says (18. p. 637) "es würde von grossem Interesse sein, zu erfahren, ob *Pipa* wirklich eine diesem Apparat entsprechende Stimme hat. Mein Freund, Freiherr A. von Klinckowström, der lebende Wabenkröten in Surinam oftmals beobachtet hat, will niemals einen Laut von ihnen gehört haben." And even in the current year Wilder writes (42. p. 291) that the matter "is deserving of careful investigation from the side of the physicist, as well as that of the naturalist." Mr. Thompson's remarks were therefore most opportune.

On further inquiry I gathered that the sounds were heard by many visitors to the Society's Gardens, who variously described them as resembling the tapping of a key on the glass of the tank in which the animals lived, the striking of two chisels together, and the distant sound of a bricklayer's trowel. All were agreed that there is a metallic ring about the sound, and that two, three, or four taps follow one another in quick succession,—then, after a pause there comes a repetition, and so on throughout the day and night. There is at present insufficient evidence that the noise is an accompaniment of the amatory overtures, but it is worthy of remark that these animals were mute before the breeding period, and have since relapsed into silence. Mr. Thompson stated it as his firm belief that both sexes shared in the clamour and that their voices were indistinguishable; but, personally, I fail to see how such a tapping sound could possibly emanate from the female larynx, where there is no backward growth, enlargement nor ossification of the arytenoids.

At this same meeting of the Zoological Society Mr. G. A. Boulenger, F.R.S., stated that the *Xenopus* during the breeding period utters a sound which he compared with that produced by

pushing the wet finger across a pane of glass. On referring to the structure of the larynx, it is evident that the sound must be produced by the vibration of the arytenoid cartilages or the edges of the glottis, since there are no vocal cords. Judging by the similarity in the shape of the arytenoids in the two sexes, it is probable that there is but little difference in the voices of the male and female.

Laryngeal Muscles of *Xenopus lævis*.

In view of the fact that the laryngeal skeleton is so dissimilar in the male and female of the two genera of the Anura Aglossa, it is not surprising that the muscles in relation with it should also differ in a remarkable degree. The following pages contain an account of the laryngeal muscles of both sexes of *Xenopus* and of the female *Pipa*. The specimens of male *Pipa* at my disposal were all unsuited for an examination of the muscular system, but I regret this the less as, thanks to Grönberg, our information on the laryngeal muscles of the male *Pipa* is not deficient. The object of this portion of the investigation was not only one of correlation of the various muscle-masses occurring in the two sexes of the same species, and of comparison of the muscles of *Pipa* with those of *Xenopus* and the tongued Anura, but of the search after additional evidence of the homology existing between the parts of the laryngeal complex of the two aglossal forms and those of the hyobranchial and laryngeal skeleton of more normal batrachians. As has already been pointed out by Henle (19. p. 24), muscles running normally from the hyobranchial skeleton to the larynx become in *Xenopus* and *Pipa* intrinsic laryngeal muscles, owing to the annexation by the larynx of a part of the hyobranchial skeleton. And some of the trunk muscles attached in other Anura to the hyobranchial skeleton here become extrinsic laryngeals.

The first account of the laryngeal muscles of *Xenopus* we owe to Mayer (26. p. 30). His description, which refers to the male, is unaccompanied by illustrations. Henle followed, four years later, with observations on the female, giving figures of the intrinsic muscles of the larynx. Beddard has recently described the muscular anatomy of both *Pipa* (1) and *Xenopus* (2) in greater detail than had been done previously; but he does not allude to the laryngeal muscles of either genus. The information furnished recently by Wilder concerning the laryngeal muscles of *Xenopus*

is of a very fragmentary and unreliable character, but he excuses himself (42. p. 309) on the ground that his only material consisted of a series of sketches drawn from a specimen dissected several years before. His figures (42. Taf. 21. figs. 58 and 61) are presumably reproductions of these sketches.

Female.

Dilator laryngis (Pl. 10. fig. 2, *d*).—This dilator muscle of the glottis, called by Henle (19. p. 27 and Taf. 2. fig. 5, *m*) the "unterer Erweiterer," arises from the external and dorsal surfaces of the posterior three-fourths of the thyrohyal, and partly also from the roof of the larynx. None of the fibres arise from the floor; a point of some importance when considering sexual differences. The anterior end of the muscle runs into an extensive aponeurosis, the fibres of which pass directly inwards, in a direction transverse to the long axis of the larynx, and, after passing over the 'blinker-shaped' process of the laryngeal cartilage (Pl. 8. fig. 3, *bl.*), are inserted into the dorso-external edge of the massive posterior enlargements (*ar.*') of the arytenoid cartilage, and into the posterior part of the arytenoid (*ar*). guarding the glottis. The anterior part of the insertion of this muscle is not tendinous. No great difficulty besets the determination of this muscle, for, since it runs from the hinder part of the thyrohyal to the outer surface of the arytenoid, it evidently corresponds with the dilator laryngis * of other Anura.

The part of the muscle that arises from the roof of the larynx (Pl. 10. fig. 2, *d*') also spreads on to the thyrohyal, beneath the greater belly of the dilator. It is separable from the latter, and its tendon, which is about as long as the muscle itself, passes along the dorso-internal border of the thyrohyal, and, running in a groove between the roof and side of the larynx proper as around a pulley, is attached to the postero-externo-dorsal corner of the arytenoid enlargement. The relations are not such as to warrant the recognition of this as a distinct muscle. That the dilator muscle should spread from the thyrohyal inwards on to the roof of the larynx is not exceptional, for in the frog a few of the fibres of this muscle arise from the cricoid cartilage

* Dilatateur, Saint-Ange, 36. p. 421, and Pl. 26. fig. 3', *d*'.
Hyo-ex-glottique, Dugès, 10. p. 126, and Pl. vii. (bis), fig. 47, no. 26.
Oeffner des Stimmladeneingangs, Henle, 19. p. 23.
Dilatator laryngis, Ecker, 12. p. 315, and Göppert, 16. p. 63.

(see 12. p. 313). Wilder figures in *Rana clamitans* (42. Taf. 20. fig. 32, *t'*) an accessory slip of the dilator arising from the laryngeal cartilage instead of the thyrohyal, an exact counterpart of this slip in *Xenopus*.

Dilator laryngis anterior (Pl. 10. fig. 2, *d.a.*).—This muscle, the "oberer Erweiterer" of Henle (19. p. 27, and Taf. 2. fig. 5, *m'*), arises from the external surface of the anterior part of the thyrohyal and extends over rather less than one half its length. It is inserted into the dorso-external surface of the arytenoid cartilage, in a line passing obliquely across the compressor muscle (*c*), which is peculiarly modified in consequence. No sharp line of separation can be distinguished between this muscle and the dilator just described, with which its fibres form a continuous series. So far as can be made out, the junction is oblique, the hinder part of the dilator anterior overlapping the front part of the dilator. Both muscles run from the thyrohyal to the arytenoid, and the insertion of the dilator anterior is in a continuous line with that of the larger muscle (see the dotted line on the left side of fig. 2, Pl. 10). The fibres of the two muscles commingle externally as they arise from the thyrohyal, so that were it not for the greater distinctness and more marked individuality of the muscle under consideration in the male *Xenopus* and in the female *Pipa*, there would not be sufficient evidence to justify the conception of it as a separate muscle worthy of a distinctive name. It is a muscle which has arisen in all probability by the separation of the anterior part of the normal dilator laryngis, and may therefore be designated the "dilator laryngis anterior."

The only other determination which is at all plausible is that it represents the "constrictor" muscle* of other Anura, which has shifted back along the side of the glottis instead of uniting with its fellow of the opposite side in front. The constrictor normally arises from the thyrohyal and runs on the anterior side

* Hyo-pré-glottique, Dugès, 10. p. 126, and Pl. vii. (bis), fig. 47, no. 25.
Verengerer des Aditus laryngis, Henle, 19. p. 24 and Constrictor, 19. Taf. i. fig. 42, *n*.
Constrictor aditus laryngis, Ecker, 12. p. 315.
Peri-arytenoideus ventralis, Wilder, 41.
Hyo-laryngeus, Göppert, 16. p. 63.
Constrictor laryngis, Wilder, 42. Taf. 20. fig. 31, *cs*.
Saint-Ange (36) does not distinguish between the constrictor and the dilator. He calls them both "dilatateurs" (p. 421), and marks them *d* and *d'* in fig. 3', Pl. 26.

of the dilator. If this suggestion be rejected the constrictor muscle is not represented in *Xenopus* *.

Compressor glottidis (Pl. 10. fig. 2, *c*).—Lying on the right and left sides of the glottis and extending a short distance behind it is a muscle which I take to represent the compressor glottidis † of the frog, combined in all probability with the outer or posterior compressor ‡.

Henle calls it the "Compressor der Stimmlade" (19. p. 27, and Taf. 2. fig. 5, *p*). In front it is attached, close to the median line, to the upper surface of the basal plate of the hyobranchial skeleton at a short distance behind its anterior border (Pl. 8. fig. 1, *y*). The muscle passes directly backwards, external to the arytenoid, and unites, behind the glottis, with its fellow of the opposite side in a linea alba, some of the fibres being inserted directly into the glottidean portion of the arytenoid cartilage just at its junction with the massive posterior enlargement. A broad sheet of fibrous tissue extends back from the hind end of the muscles and linea alba to be inserted into the front edge of roofing cartilage of the larynx. It is probably to be regarded as an aponeurotic extension of the muscle itself. The indirect connexion thus established between the muscle and the cricoid cartilage is not without parallel, for Göppert states (16. p. 63) that in the common frog some of the fibres of the external

* Henle definitely states (19. p. 26) that the constrictor is absent in *Pipa*: he makes no mention of it in *Xenopus*. The constrictor is absent in *Bombinator* (Henle, 19. p. 24, and Wilder, 42. Taf. 21. figs. 46 and 47), a fact of some importance considering how closely the hyobranchial and laryngeal skeleton of this toad resembles that of *Xenopus*. Wilder has remarked its presence in *Alytes*, and notes that it occupies an exceptionally ventral (cardiac) position. Grönberg has recorded its occurrence in the male *Pipa*, but concerning this see pp. 90 and 91.

† Compressor, Henle, 19. p. 24, and Taf. i. fig. 42, *p'*.
Hoher, medianwärts liegender Constrictor, Ecker, 11. fig. 14, *Co.l.*
Hyo-arytenoideus anterior, Ecker, 12. p. 315, and fig. 205, *Co.l.*
Sphincter anterior, Göppert, 16. p. 63.
Compressor laryngis, Wilder, 42. Taf. 20. fig. 31, *cp*.

‡ Compressor, Henle, 19. p. 24, and Taf. i. fig. 42, *p''*.
Tiefer constrictor laryngis, Ecker, 11. fig. 14, *Co.l'.*
Hyo-arytenoideus posterior, Ecker, 12. p. 315, and fig. 205, *Co.l'.*
Sphincter posterior, Göppert, 16. p. 63.
Sphincter dorsalis, Wilder, 42. Taf. 20. fig. 31, *sf.d.*

Dugès does not discriminate between the two muscles, but applies the term hyo-post-glottique to both, 10. p. 126, and Pl. vii. (bis), fig. 47, no. 27.

Saint-Ange calls them both constricteurs, 36. p. 421, and Pl. 26. figs. 3', 4' and 5', *c* and *c'*.

division of the compressor (his "sphincter posterior") arise from the cricoid cartilage, a fact which Henle had previously recorded (19. p. 24) but in a somewhat unsatisfactory manner.

The middle of the compressor muscle is tendinous and closely bound to the external face of the arytenoid over a narrow area extending backwards and outwards from the middle of the length of the glottis. While the dilator anterior muscle is to all intents and purposes connected with the arytenoid cartilage, it would be more correct to say that it is inserted into the tendinous middle tract of the compressor, which in its turn is bound to the arytenoid. For, when the compressor is removed bodily from the skeletal parts, the dilator anterior muscle is found to be still very tightly bound to it, showing that the fibres do not simply decussate. The same treatment also shows that the two bellies, anterior and posterior, of the compressor cannot well be regarded as distinct muscles. Under any circumstances, they cannot be individually homologous with the two muscles running alongside the glottis in the frog, although the digastric compressor of *Xenopus* is probably equivalent to the two muscles of the frog taken collectively.

The muscles in the immediate vicinity of the glottis in Anura are subject to extreme variation, even in genera which are admitted to be closely allied. Henle made a comparative study of these muscles, and Wilder has latterly reconsidered the subject. Wilder acknowledges that the study is a most confusing one; but he has arrived at the conclusion (42. p. 308 *et seq.*) that the primitive periglottidean muscle in Anura is a sphincter surrounding the arytenoid cartilages and unconnected with the thyrohyals. The muscle may remain as such unchanged (*Bombinator* *), or part of it may become differentiated into a compressor and a constrictor, while part remains as a sphincter (*Rana*); or the entire muscle may differentiate into compressor and constrictor (*Bufo*). The compressor and constrictor both acquire a secondary connexion with the thyrohyal. Of *Xenopus* he says (42. p. 313), "The sphincter in *Dactylethra* appears very simple, divided into four quarters by median and lateral raphés," and he notices that the "lateral raphés appear to be connected with the

* Henle is in error in describing (19. p. 24) a connexion between the compressor muscle and the hyobranchial skeleton in *Bombinator* and *Discoglossus*. I have examined the muscle in these genera and find it to be an intrinsic laryngeal in both.

method of insertion of the Dilatator." He fails, however, to note that the anterior ends of the sphincter muscles are attached, not to the arytenoid cartilages or one to another, but to the portion of the hyobranchial cartilage between the anterior ends of the thyrohyal bones. This fact leads me to think that the periglottidean muscles of *Xenopus* are not so simple as he makes out, and that they do not represent an undifferentiated sphincter such as occurs in *Bombinator*. Wilder says (**42**. p. 307) that in a late larval stage of the tadpole of *Rana* the as yet undivided sphincter attaches itself to the inner edges of the two thyroid processes. This occurs before the constrictor and compressor have been differentiated, and it is just this stage of development which, I take it, persists in *Xenopus*. The periglottidean muscle of *Xenopus* may therefore be regarded as including an undifferentiated constrictor; and the absence of any muscle which can with certainty be regarded as the constrictor laryngis lends support to the view.

Hyoglossus.—Turning now to the ventral aspect of the larynx, three important muscles are to be noted:—the hyoglossus, the geniohyoideus internus, and the petrohyoideus. The hyoglossus (Hyoglossus, Henle, **19**. p. 26) consists of three separate bellies, the external of which (hyoglossus externus, Pl. **10**. fig. **1**, *h.e.*) arises from the ventral surface of the thyrohyal at about the middle of its length; while the middle division,—which Henle (**19**. p. 26) erroneously declares to be absent in *Xenopus*, although he mentions it as occurring in *Pipa*,—takes its origin from the floor of the larynx at about one-third of the length from the anterior end (fig. 1, *h.i.*). Mayer (**26**. p. 30) calls the hyoglossa muscle of Anura the ceratoglossus, and states that it appears to be wanting in *Xenopus*,—clearly an error of observation. He considers it equivalent to the muscle which he had previously called the laryngoglossus in *Pipa* (**25**. p. 537, and fig. 2, *e*).

The middle division of the muscle, the hyoglossus internus, is really double, and the two halves are at their origin perfectly distinct. But anteriorly they unite in the median plane, and at the front of the larynx they are inseparable. The external divisions arising from the thyrohyals, although closely applied to the internal division, do not fuse with it. The three muscle-trunks, after running forward ventral to the laryngeal cartilage and dorsal to the m. geniohyoideus internus (Pl. **10**. fig. 1, *g.i.*), are still readily separable as they pass upward, immediately in

front of the basal plate, to be distributed to the mucous membrane occupying the position of the lost tongue. It is on the relations of its anterior end that we have to rely for an identification of this muscle as the hyoglossal, for the origin posteriorly is quite exceptional. The hyoglossus in tongued Anura arises from the posterior extremity of the thyrohyal. In *Xenopus*, therefore, the muscle has undergone considerable diminution in length, arising as it does from the middle of the length of the bone. The hyoglossus internus is not represented in other Anura, and it is all the more curious to note that in the male *Xenopus* the normal external trunks have disappeared, leaving only this exceptional median portion.

Petrohyoideus (Pl. 10. fig. 1, *p*).—Arising from the posterior part of the ventral surface of the larynx close to the median line, and running out sideways, is a peculiar muscle which represents the petrohyoideus of more familiar Anura *. It occurs in both sexes of *Xenopus*, in the female *Pipa*, and probably also in the male. Mayer and Henle are silent concerning it: in fact, throughout the whole of the literature on *Pipa* and *Xenopus* that I have examined, I have met with no reference to such a muscle. The muscle spreads beneath the ventral surface of the larynx in a fan-like manner, breaking up into small bundles of fibres which alternate more or less regularly on the right and left sides. The number of radiating bundles is subject to considerable variation, in some specimens being as small as three, while in one larynx examined as many as seven distinct divisions could be recognized on one side and six on the other. The muscle passes out sideways, ventral to the geniohyoideus internus, and diminishes considerably in width. Then, remaining of the same diameter for the rest of its length, it takes a circuitous course and is ultimately attached to the back of the auditory region of the skull. There is, I think, sufficient evidence here for identifying the muscle with one of the posterior petrohyoids of the frog, most probably the third or fourth of those described by Ecker (12).

Geniohyoideus.—The geniohyoideus has already been described by Henle (19. p. 26) as double in *Xenopus*. The outer division, geniohyoideus externus, arises from the mandible a short distance from the symphysis, and is inserted into the ventral surface of

* Masto-hyoïdien, Dugès, 10. p. 125, and Pl. vii bis, fig. 44, nos. 20, 21, 22.
Stylohyoideus, Walter, 40. p. 36.
Petrohyoideus, Ecker, 12. p. 66, and figs. 60, 61, and 205, *p.h.*

the ala of the hyobranchial skeleton, at about the level of the anterior ends of the thyrohyals, in the position marked *g.e.* in fig. 1, Pl. 8. This external geniohyoid of *Xenopus* is called by Mayer (**26**. p. 30) the genioceratoideus, but he considers it homologous with the muscle which he had previously named the geniohyoideus in *Pipa* (**25**. p. 538). The geniohyoideus internus (Pl. **10**. fig. 1, *g.i.*) (geniohyoideus of Mayer, **26**. p. 30) is attached by its anterior extremity to the mandible, nearer to the symphysis than the externus, runs parallel with the latter and extends backwards below the larynx to be inserted into the ventral surface of the posterior epiphysis of the thyrohyal. It runs ventral to the hyoglossus, but dorsal to the petrohyoideus. The two internal geniohyoid muscles are in close contact with one another for the greater part of their length, but they diverge somewhat posteriorly. In the frog, the geniohyoideus has a single belly in front and divides posteriorly into two parts. The internal of these (geniohyoideus medialis of Walter, **40**. p. 32) is attached to the inner border of the anterior end of the thyrohyal, and the outer (g. lateralis of Walter, **40**. p. 33) to the hinder of the two lateral cartilaginous processes of the body of the hyoid. If we admit that these two divisions of the muscle correspond with the geniohyoideus internus and externus respectively of *Xenopus*, a perfectly legitimate supposition, we must not fail to notice that the internal division is attached in *Xenopus* to the posterior epiphysis of the thyrohyal, but in the frog to the anterior end of that bone.

Obliquus internus.—The anterior end of the internal oblique muscle, though inserted mainly into the ventral surface of the great wing of the hyobranchial skeleton, sends a small slip with tendinous extremity to the posterior end of the thyrohyal (Pl. 10. fig. 2, *o.i.*). The incorporation of the thyrohyal into the laryngeal complex of *Xenopus* demands that this slip should be regarded as a laryngeal muscle, and a passing notice is therefore here accorded to it.

Male.

In considering the muscles of the male *Xenopus*, it will be sufficient to note only those points in which they differ from the muscles of the female. The same seven muscles are in relation with the larynx, although they are very much modified in form. The trend of such modification is not in one uniform direction, for, while the dilator muscles are excessively enlarged as compared with those of the female, the geniohyoideus internus, the

petrohyoideus, and the hyoglossus are considerably reduced. The most remarkable feature is, without doubt, the extensive development of the *dilator* (Pl. 10. figs. 3 & 4, *d*). This muscle covers the whole of the sides of the laryngeal complex, nearly the whole of the ventral surface, and a considerable portion of the dorsal. It is distinctly differentiated into a superficial and a deeper layer (*d* and *d'*), and the tendon of the latter passes forward and inward in the pulley-like groove at the side of the roof of the larynx, and is inserted into the dorso-external border of the posterior massive part of the arytenoid. The aponeurosis that passes over the blinker-shaped process of the laryngeal cartilage is very delicate, far more so than in the female. The dilator muscle in the female extends round the outer border of the thyrohyal and very slightly, if at all, on to its ventral surface; but in the male the belly of the muscle has spread so as to cover the whole of the ossified part of the thyrohyal and to meet its fellow of the opposite side in the ventral median line (see Pl. 10. fig. 3). The only parts of the ventral surface of the larynx over which the muscle does not extend are, first, a small triangular area in front occupied by the hyoglossus, and, secondly, a larger space, also triangular, at the posterior end between the petrohyoids.

The *dilator anterior* (Pl. 10. fig. 4, *d.a.*) is better differentiated from the dilator than in the female, although relatively shorter and smaller in bulk. Its fibres are inserted into the arytenoid cartilage over the anterior two-thirds of the side of the glottis. They pass outward and downward, but very slightly backward, and spread out in the form of an aponeurosis over the ventral surface of the anterior part of the dilator. Wilder (42. Taf. 21. fig. 61, *t*) identifies this muscle as the "dilatator laryngis." He describes it, however, as arising from the thyrohyals, an origin peculiar to the female; and I cannot help thinking that he was mistaken in the sex of the animal he examined. The *hyoglossus* (Pl. 10. fig. 3, *h.i.*) is much more feebly developed than in the female, and although the relations of the anterior end are the same, the posterior extremity does not reach nearly so far back. In the female the outer fibres arise from the thyrohyals, but in the male the whole of the muscle arises from the cartilage of the laryngeal floor. The reduced hyoglossus thus probably corresponds with the median belly only (hyoglossus internus) of the muscle in the female. The *geniohyoideus internus* (Pl. 10. fig. 3, *g.i.*) is more

slender than in the female, but exhibits, even in a more marked degree, the same diminution in width in that part of its length which underlies the anterior end of the larynx. It runs dorsally to the petrohyoideus as in the female, but is separated from the cartilaginous floor of the larynx by the intruded sheet of the dilator.

The *petrohyoideus* (Pl. **10.** fig. 3, *p*) is also more feebly developed than in the female. Only the anterior fibres reach the median line, so that a triangular space of bare cartilage is left between the hinder parts of the expanded laryngeal extremities of the muscle. The radiation of the fibres is much more uniform and regular than in the female. The *compressor glottidis* (Pl. **10.** fig. 4, *c*) does not differ materially from that of the female. Many of the fibres are distinctly attached to the arytenoid cartilage posteriorly, and the connexion of the muscle with the fascia-sheet covering the dorsal surface of the arytenoid plate (Pl. **8.** fig. 6, *ar.'*) is comparatively unimportant. Owing to the feebleness of the anterior dilator, the anterior and posterior bellies of the compressor are less distinct than in the female, and, when the muscle is isolated and examined under the microscope, muscle-fibres can be seen passing from one belly to the other. In the female, the intervening part is wholly tendinous.

Laryngeal Muscles of *Pipa americana*.

The first description of the hyobranchial and laryngeal muscles of *Pipa* we owe to Mayer (**25**), who includes them in his chapter on the general muscular anatomy of the female. Meckel (**28**) paid some attention to the subject, as also did Henle (**19**). Henle's description applies to the female sex *, and is well illustrated. More recently, Grönberg (**18**. pp. 637 and 638) has resumed the study of the subject, but his remarks refer exclusively to the intrinsic muscles of the male larynx. His figures (Taf. 38. figs. 18–20) are, however, most valuable, being the only illustrations extant of the laryngeal muscles of that sex.

Female.

The muscles in relation with the larynx in the female *Pipa* resemble in the main those of *Xenopus*. The same arguments, therefore, which have previously been adduced for determining

* Not male, as stated by Grönberg (**18**. p. 637).

the homologies of the muscles of *Xenopus* with those of other Anura will apply in the present case, and need not be repeated. The most important feature in which the laryngeal musculature of *Pipa* differs from that of *Xenopus* is in the absence of the geniohyoideus internus. Arising from the roof of the larynx in the elliptical area marked *a* in fig. 5, Pl. 10, is a very loose tissue, mainly connective tissue, but containing numerous scattered muscle-fibres which are inserted into the mucous membrane of the pharynx behind the glottis. No particular direction can be ascribed to the fibres, for they cross one another in a most irregular manner. Radiating outwards and backwards from the postero-external border of the same area are a few muscle-fibres arranged in the form of a thin sheet, attached distally to the internal concave edge of the great wing of the hyobranchial skeleton. Neither of these tracts appears to be of sufficient importance to warrant the application of a distinctive name.

The *dilator laryngis* (Pl. **10**. figs. 5 & 6, *d*) [Laryngeus proprius, Mayer, **25**. p. 538; Dilatator aditus laryngis, or Erweiterer, Henle, **19**. p. 26, and Taf. 2. figs. 14, 15, & 23, *m*] arises from the postero-external border of the laryngeal complex, and, considering the large size of the muscle, its posterior attachment is remarkably small. It occurs partly on the dorsal and partly on the ventral surface of the larynx. Its belly is large and well defined, and narrows considerably anteriorly, and it is inserted by a small tendinous extremity into the most external part of the lateral promontory of the arytenoid cartilage (Pl. **9**. fig. 2, *d*). The *dilator laryngis anterior* (Pl. **10**. fig. 5, *d.a.*) is very clearly distinguishable from the dilator. It arises from the fascia of the external surface of the anterior part of the latter muscle, passes upwards, forwards, and inwards, and gradually diminishes in width. It runs dorsal to the compressor (*c*) and is inserted into the edge of the arytenoid cartilage guarding the side of the glottis. A few of the fibres, also, are attached indirectly to the arytenoid cartilage by being inserted into the aponeurosis between the anterior and posterior bellies of the compressor.

Compressor glottidis (Pl. **10**. fig. 5, *c*) [Compressor laryngis, Henle, **19**. Taf. 2. figs. 14, 15, *p*].—The anterior and posterior bellies of this muscle are very sharply differentiated, and the aponeurosis between the two extends obliquely backwards and outwards, exactly as in *Xenopus*. The aponeurosis is attached by its ventral surface to the anterior edge of the lateral pro-

montory of the arytenoid, and by its dorsal surface to some of the fibres of the dilator anterior. Posteriorly, the compressor muscles of the right and left sides unite, immediately behind the glottis, in a linea alba which extends backwards for a distance equal to the width of each muscle. The anterior extremity of the compressor is attached to the lateral edges of the median isthmus of cartilage (Pl. 9. fig. 1, *i*) which connects the part of the hyobranchial cartilage bounding the hyoglossal foramen with that which forms the anterior end of the laryngeal complex. In this respect the compressor differs from that of *Xenopus*, for in this latter genus the attachment of the anterior end of the muscle is to the dorsal surface of the equivalent cartilage.

The *hyoglossus* [Laryngoglossus, Mayer, **25.** p. 537 and fig. 2, *e*; Rückwärtszieher der Zunge, Meckel, **28.** Theil iv. p. 340; Hyoglossus, Henle, **19.** Taf. 2. figs. 22 and 23, *4*] is a much longer muscle than that of *Xenopus*, and extends nearly the full length of the larynx. The external and internal divisions also are better differentiated. The hyoglossus internus (Pl. **10.** fig. 6, *h.i.*) arises from the ventral surface of the larynx near the posterior end, and the area of attachment slopes obliquely backwards and outwards. The muscle crosses dorsally to the petrohyoideus and runs forwards beneath the larynx, diminishing at the same time in width. The internal hyoglossals of the right and left sides converge anteriorly; they fuse together, pass through the median foramen in the hyobranchial skeleton, and spread out as a single muscle (Pl. **10.** fig. 5, *h.i.*). This is inserted into that part of the mucous membrane of the floor of the mouth which lies over the beak or point of the hyobranchial skeleton (Pl. 9. fig. 1, *ch.'*). The external hyoglossus (Pl. **10.** fig. 6, *h.e.*) is in the main slightly broader than the internal, but its posterior area of attachment is smaller than, and lies posteriorly to, that of the latter. The two muscles, internal and external, thus overlap one another at their posterior ends, but they separate out anteriorly. The external trunks occupy a lateral position with regard to the internal as they pass through the hyoglossal foramen. Then, instead of continuing forwards, they turn sharply outwards at right angles to their former course (Pl. 10. fig. 5, *h.e.*), the left to the left and the right to the right. They spread out and become inserted into the mucous membrane of the lateral parts of the floor of the mouth. Henle (**19.** p. 25) mentions the three muscles spreading out in the floor of the mouth, but he fails to note the

quadruple nature of the hyoglossal muscle posteriorly. He also states (p. 77) with Mayer (25, p. 537) that the external hyoglossus arises from the thyrohyal or columella. Careful dissection, however, shows that the origin is internal to the cartilage which is to be regarded as the epiphysis of the thyrohyal.

The *petrohyoideus* (Pl. 10. fig. 6, *p*) arises from the membranous ventral wall of the larynx, close to the median line, at about one-third of the length from the posterior end. It extends outwards and backwards, coils round the external edge of the great wing of the hyobranchial skeleton, and, passing forwards and upwards, is attached to the dorso-external crest of the auditory capsule, close beside the inner end of the columella auris. It runs ventral to the hyoglossus and the geniohyoideus externus, but dorsal to the obliquus internus. It is a very long and meandering muscle, and is of uniform width all along, except at its laryngeal extremity. It is relatively smaller than in the female *Xenopus*.

Geniohyoideus (Mayer, 25. p. 538; Henle, 19. Taf. 2. figs. 22 and 23, *3*).—Henle (p. 26) has already noted that the inner division of the geniohyoideus, attached to the laryngeal skeleton in *Xenopus*, is absent in *Pipa*. The external division is a long, slender muscle, of even diameter, extending from the symphysial region of the mandible to the postero-external region of the ventral surface of the great hyobranchial ala. The position of its insertion is shown at *ge.* in fig. 1, Pl. 9. The recognition of this muscle in the embryo is a matter of no great difficulty, and as soon as the wing of the hyobranchial skeleton is clearly differentiated from the neighbouring parts, the insertion of the muscle is seen to be related to it exactly as in the adult (see Pl. 11. fig. 8, *ge.*). Seeing that the wing is purely a derivative of the hypobranchial plate of the larval skeleton, it would be more satisfactory to substitute for geniohyoideus the word geniohypobranchialis, the name by which Schulze (38) designates this muscle in his treatise on the development of *Pelobates*. It is worthy of remark that, while in *Pipa* the geniohyoideus externus is attached to the ala near its posterior edge, the position of the insertion of this muscle in *Xenopus* lies in front of the line joining the anterior extremities of the thyrohyals (see *ge.* Pl. 8. fig. 1 and Pl. 9. fig. 1).

Obliquus internus (Pl. 10. fig. 5, *o.i.*).—In the larynx of the young but sexually mature female depicted in fig. 5, Pl. 10, the laryngeal division of the internal oblique muscle is of consider-

able size. It partially overlaps the dilator muscle and is inserted into the dorsal surface of the larynx. In older specimens, however, the greater part of the muscle becomes transformed into a fatty substance of a dark brown colour, similar to that which occurs in abundance around the pointed cartilage at the front of the hyobranchial skeleton and on the underside of the alæ. Such part of the muscle as remains unchanged is attached to the postero-lateral corners of the laryngeal skeleton, in the position already recorded for it by Mayer (**25.** p. 536) and Henle (**19.** p. 26 and Taf. 2. figs. 14 and 23, *7*). At no age does the muscle develop a tendinous extremity as it does in *Xenopus*.

Male.

For details of the laryngeal muscular system of the male *Pipa* I have been obliged to rely entirely on the account given by Grönberg, for both Mayer's and Henle's descriptions of these muscles refer to the female, and although I have had access to three specimens of the male, they were all unsuitable for a careful examination of their muscular anatomy. Grönberg describes (**18.** p. 638) four intrinsic muscles of the larynx. For the muscle around the glottis he accepts Henle's name Compressor: it appears to correspond exactly with that muscle which in the female I have called the compressor, so that it is unnecessary to discuss it further. The other three, however, open up debatable points. They arise from the sides, roof and floor * of the larynx, and extend nearly its full length; and their bellies are so united that Grönberg confesses his inability to decide whether they are three originally distinct muscles, or whether they are divisions of the same muscle, its tendon having split into three. He elects to adopt the former view. The tendon of the most dorsally-lying muscle (**18.** Taf. 38. figs. 19 and 20, *S 1*) is attached to the arytenoid cartilage guarding the glottis, and this muscle he identifies as the "dilatator laryngis" of *Rana*. The tendon of the ventrally-disposed muscle (**18.** figs. 18 and 20, *S 3*) runs to the external promontory of the ossified part of the arytenoid, and the contraction of the muscle serves to approximate the bony arytenoid rods lying in the laryngeal cavity. Since Grönberg regards these ossified parts as external arytenoids not represented in other Anura, he is

* Henle (**19.** p. 26) states that in the male *Pipa* the whole of the ventral surface of the larynx is covered by muscle, an observation which is not borne out by Gronberg's figure (**18.** Taf. 38. fig. 18).

forced to conclude that the muscle also is unique. He does not suggest any name for it. The third muscle overlaps the other two on the external or lateral surface of the larynx, and its tendon (18. fig. 20, *S 2*) unites antero-ventrally to the glottis with its fellow of the opposite side. From these relations he considers it to represent the "hoher, lateralwärts liegender Constrictor des Larynx" of Ecker (11. p. 31, fig. 14, *c.a.l.*) (called in the English edition the "Constrictor aditus laryngis," 12. p. 314, fig. 205, *c.a.l.*).

On comparing Grönberg's figures of the male with mine of the female, it will, I think, be evident at a glance that the dorsal muscle, the tendon of which he marks *S 1*, is that which I have called the dilator anterior (Pl. **10.** fig. 5, *d.a.*). The tendon in both cases is inserted into the edge of the arytenoid cartilage at the side of the glottis, and it is quite possible to conceive that the muscle has assumed a more antero-posterior direction in the male, in consequence of the glottis opening directly forwards, towards the aperture of the mouth, instead of upwards as in the female. The other two, *S 2* and *S 3*, I take to correspond with my dilator laryngis. Although in both sexes of *Xenopus* the insertion of the dilator lies entirely behind that of the dilator anterior (Pl. **10.** figs. 2 and 4), yet in the female of *Pipa* the attachment of the tendon of the dilator to the promontory of the arytenoid is situated farther forward than the insertion of the anterior dilator into the side-wall of the glottis (Pl. **10.** fig. 5). Assuming, as I think we are justified in doing, that the promontory of the female arytenoid (Pl. **9.** fig. 2, *d*) is equivalent to the similar promontory of the male which Grönberg marks *a* in his figures 10, 11, 13, and 14, it is but logical to regard his ventral muscle, *S 3*, and my dilator laryngis as identical. This leaves only his muscle *S 2* unaccounted for.

I have not been able to recognize in the female *Pipa* any third dilator, nor any union of tendons anterior to the glottis; but in both sexes of *Xenopus* there is an imperfectly differentiated slip of the dilator (Pl. **10.** figs. 2 and 4, *d'*), the tendon of which is elongated and inserted into the massive part of the arytenoid. It is true that in *Xenopus* the insertion of the slip is far behind that of the dilator anterior and the glottis, but an examination of fig. 5, Pl. **10**, will show that a similar slip differentiated from the more dorsal part of the dilator, on the rotation of the glottis forwards, would come to occupy the position of Grönberg's *S 2*.

It now only requires an extension of the tendons to meet below the glottis to complete the resemblance. The changes in the relative positions of the bellies of the muscles would follow as a consequence of the rotation of the glottis. The dilator anterior would straighten out and occupy a dorsal position, leaving the greater dilator on the ventral surface of the larynx and its accessory slip laterally. As an alternative view, it may be suggested that the ventral muscle, *S 3*, which Grönberg says is absent in the frog, is the equivalent of that curious muscle which in *Discoglossus* and *Alytes* runs from the *ventral* surface of the posterior epiphysis of the thyrohyal to the ventro-anterior point of the arytenoid cartilage. Wilder figures the muscle in *Alytes* (42. Taf. 20. figs. 36 and 37) and regards it as the displaced constrictor laryngis, which otherwise must be admitted to be absent. Whether Wilder's interpretation is correct must remain for future investigation to decide: the two muscles do not unite in front of the glottis as do the constrictors of the frog.

These conclusions savour, no doubt, of conjecture, being based on the study of figures only, drawn by two different authors, each of whom has examined the muscular system of one sex only. In spite of the interesting union of the tendons *S* 2 antero-ventrally to the glottis, I am not disposed towards an unqualified acceptance of Grönberg's determination of the muscles as the constrictors of the common frog. An exhaustive study of the muscles, extrinsic as well as intrinsic, of the larynx of the male and female *Pipa* would most assuredly repay any investigator fortunate enough to have the necessary material at his command.

Development of the Hyobranchial and Laryngeal Skeleton.

The development of the hyobranchial and laryngeal skeleton of the Aglossa is practically unknown. Parker's treatise on the development of the skull of *Xenopus* and *Pipa* (33) is the only work to which we can turn for information; and this does not furnish much. On comparing the hyobranchial skeleton of the tadpoles of *Rana*, *Alytes*, *Pelobates*, and *Bufo*, one is struck by the uniformity of structure that exists in the different genera during the earlier stages of development; and the observations now to be recorded show that the skeleton of *Xenopus* and *Pipa* conforms to the general ground-plan. The various modifications

that render it so aberrant appear only during and after metamorphosis. This is of course the conclusion one would expect to arrive at; but hypotheses, conjectures, and arguments are of infinitesimal value compared with ocular demonstration of fact.

Concerning the methods adopted in this portion of the research, extensive preliminary trials were made on the tadpoles of the common frog and of *Alytes*, with a view to discovering the method which would demonstrate the facts in the most intelligible manner, and yet leave the skeleton in a condition in which it may be preserved for subsequent examination. The easiest methods of preparation are those which fail to satisfy the second condition. The steeping of the body in water at a temperature of about 80° C., a method largely used for the preparation of the skeleton of Elasmobranch fishes, was rejected at once on account of the shrinkage and distortion which it occasions. Putrefactive maceration, which may sometimes be employed with advantage in the preparation of cartilaginous skeletons, was found unsatisfactory on account of the tendency which the delicate skeleton showed to fall to pieces, and the possibility of loose cartilages becoming lost or overlooked—objections from which the hot-water method is not free. As I had previously found the method of staining with borax-carmine and clarifying with clove-oil of the greatest value when studying the carpus and tarsus of Anura, larval as well as adult (23), I applied the process to the branchial skeleton; but had to discard it on account of the resulting brittleness of the tissues. Clarifying by glycerine and caustic potash I also tried; but the preparations made in this way cannot be kept permanently in the clarifying fluid, since the potash brings about the ultimate disintegration of the cartilages. Parker's method, of staining with an ammoniacal solution of carmine and then steeping in glycerine, is open to less objection than the preceding methods; but it resembles them all in being inapplicable at the critical period when the cartilages are becoming absorbed,—the most important stage of all. All methods involving clarification and the use of transmitted light fail utterly here. I was therefore forced to fall back on the very simple expedient of dissecting the parts under a simple microscope by powerful reflected light: a tedious and delicate operation, it is true; but with fine instruments, combined with a knowledge, to be gained only by experience, of the relative toughness of muscle, perichondrium, and cartilage, the difficulties can be overcome.

A short trial was given of that method of investigation which is now finding such favour with embryologists, and which has been employed with such excellent results by Gaupp (14) in his investigations on the hyobranchial skeleton of *Rana fusca*. The head or other part is cut into microscope-sections of known thickness, and the organs to be studied are reconstructed therefrom in wax plates, the thickness of which is the same multiple of the original as the linear magnification. The wax sheets are then pressed together, and an enlarged model of the organs is thus obtained. Without in the least wishing to depreciate the results of Gaupp's investigations, for which I have the greatest admiration, I would point out that at the critical periods, when the cartilages are forming or are becoming absorbed, their outline is extremely difficult to make out in sections, and that in fashioning the wax plates it is very largely a matter of personal opinion to decide where the line shall be drawn between the cartilage and the surrounding tissues; and thus an error of a centimetre or more, according to the magnification, may very easily creep into the model. If the sections are cut thin, this difficulty of discrimination increases; while if the sections are thick, it is almost impossible to represent truthfully in the model narrow rod-like structures which make a small angle with the planes of section. The method is even more tedious than that of actual dissection by reflected light, and far less satisfactory and conclusive.

I had already completed this portion of the investigation by the time that Wilder's paper (42) reached me; and so I did not include a trial of the method he adopted in his recent work on the adult laryngeal skeleton of Amphibia, viz., that of mounting in turpentine and Canada balsam after slow staining with a weak alcoholic solution of methyl-blue, washing, and dehydrating. I have since made a few experiments in this direction, and can testify to the differentiating action which the dye has upon hyaline cartilage. The method, however, is useless for the demonstration of cartilage which is just forming or is undergoing absorption, and could not therefore be applied successfully to such purposes as the present.

Xenopus lævis.

Of the large number of tadpoles of *Xenopus* examined, it must suffice to choose only three stages for minute description and delineation, because in the earlier stages of development the

hyobranchial skeleton undergoes but little change, and that very slowly; and because the later stages, at which the metamorphosis is actually taking place, I have been unable, in spite of strenuous endeavours, to procure. I have already delayed the publication of this paper several months in the hope of being able to obtain the latter stages; but as there seems to be no prospect of achieving this in the near future, I submit such results as I have already obtained. For most of the specimens examined I am indebted to the generosity of Mr. G. A. Boulenger, F.R.S.

In making comparison of different tadpoles of the same species, I find that actual size is no criterion of the degree of development, since so much depends on the favourable or adverse conditions of life. The carefully recorded measurements of Parker's *Xenopus* larvæ were useless to me for correlating his tadpoles with mine. The only reliable data are afforded by the extent of development of the paired limbs. The oldest of the three chosen stages (Stage III.) is characterized by the presence of all four limbs, the fore as well as the hind being well developed, and by the possession of a large tail which shows no signs of absorption. The larvæ of the second stage have the hind limbs powerfully developed; but the fore limbs are only half as large as in Stage III. The first stage is a most comprehensive one, including tadpoles with hind limbs well developed and with the fore limbs recently extruded; tadpoles with hind legs not yet markedly flexed and with no trace of fore limbs; tadpoles with the hind legs just appearing on the surface of the body; and tadpoles with no traces of paired limbs at all. There is no appreciable difference beyond one of size in the hyobranchial skeleton of any of these tadpoles of Stage I.; but a trifling variation can be discerned in the relative size of the larynx.

In the figures of the developing hyobranchial skeleton (Plate 11) the mandible is included, because it serves to give an idea of the size of the mouth at each stage—a most desirable item of information,—and because it demonstrates the relative hugeness of the hyoid arch, and shows that while the hyoid and mandibular arches are closely approximated in *Xenopus*, they are widely separated in the corresponding stages of *Pipa*. The ossifications in the mandible are not indicated in the figures. Parker shows (**33.** Pl. 56. fig. 6, and Pl. 58. fig. 4) a pair of "mento-meckelian" or "inferior labial" cartilages in the symphysial region of the mandible of the early larva of *Xenopus*. In this

position, however, I find not a pair of cartilages, but a single median piece which shows signs of division into two only in the third stage of development. This cartilage I take to be an integral part of the mandibular arch—in fact, the median inferior element or basimandibular. An examination of the first stage especially shows that, although the inferior portions of the mandibular and hyoid arches are so dissimilar in size, they are built essentially upon the same plan, and consist each of a pair of ceratal elements and a median basal piece (see Plate 11. fig. 1). In this respect the mandibular arch of *Xenopus* exhibits the retention of a most primitive character.

The above interpretation of the symphysial cartilage opens up the question of the morphological value of mento-meckelians in general; and I am inclined to think that, in Anura at least, the symphysial cartilages or bones are not labials developed, as the upper labials undoubtedly are, in special relation with the suctorial lips, but the modified right and left divisions of a median basimandibular. The mouth of the young *Pipa* and *Xenopus* is not suctorial, but has the form of a wide slit from the very first; and this fact it is which gives the young of the Aglossa such a fish-like appearance. I have not been able to satisfy myself concerning the presence of mento-meckelian cartilages in *Pipa*. The mandible exhibits a symphysial segmentation as early as Stage II. (fig. 5); and at Stage VI. (fig. 9) the two rami are as distinct as in the adult. As already shown by Parker (33. pp. 638, 651, and 655), no symphysial elements are to be recognized in the adults of either *Xenopus* or *Pipa*.

STAGE I. (Plate 11. fig. 1.) *Tadpoles ranging from those in which the hind legs are just appearing, to those with the fore legs recently extruded.*

The branchial skeleton has attained its maximum larval development; but it as yet shows no signs of absorption. On comparing the hyobranchial skeleton of *Xenopus* at this stage with that of a more familiar anurous batrachian, e. g. *Rana* or *Alytes*, one cannot fail to notice how small are the three branchial clefts in proportion to the large expanse of the branchial cartilage. Instead of four elongated bars of cartilage on each side, connected distally by an epibranchial marginal bar, and confluent proximally with a cartilaginous hypobranchial plate, we have rather a pair of greatly inflated cartilages of considerable size,

each approximately resembling in shape the half of a longitudinally divided egg-shell. The cartilage is thin and fairly uniform throughout, and is perforated ventrally by the three branchial slits sloping obliquely outwards, backwards, and slightly upwards. The two cartilages are closely applied one to another in the median plane for about one-half of their length. Their applied faces are nearly flat, and are readily separable, no fusion having yet taken place. The two cartilaginous basket-works look upwards and slightly inwards, and the inner and anterior edges are involute. Of the three branchial clefts the first is situated about halfway from the anterior end, so that in front of it there is quite a large extent of unbroken cartilage. This latter represents the first branchial arch of the tadpole of the frog. The length of the most anterior cleft is about one-half of the transverse diameter of the basket. The second and third clefts are nearly parallel with the first: they are successively shorter, and lie rather closer to the median line. The two bars of cartilage separating the three clefts are the second and third branchial arches, while the cartilage bounding the last cleft posteriorly represents the fourth branchial arch of the frog-tadpole. Seeing that in fishes the cleft is situated in front of the arch of the same denomination (*i. e.* that the first branchial cleft is bounded behind by the first branchial arch, and so on), the three clefts here present represent the second, third, and fourth branchial clefts respectively. It may seem unnecessary to insist on this point; but when three clefts occur, as here, in a continuous cartilage, there is a temptation to speak of them loosely as the first, second, and third, and then arises a danger of losing sight of their morphological enumeration.

The inner or pharyngeal surface of the branchial cartilage is not smooth, but is covered with a multitude of minute, blunt, arborescent growths. These are not shown in the figures. There are also sharply defined ridges running along the upper surface of the second and third branchial arches, and continued over the undivided cartilage both outwards, backwards, and upwards, to the external edge, and inwards, forwards, and upwards, to the internal overhanging border. These latter processes are evidently equivalent to those outgrowths in the branchial apparatus of the *Rana* tadpole which Gaupp calls spicula ii. and iii. (14. Taf. xvii. fig. 1), and to which Parker (34) attaches undue importance by calling them the true branchial arches. The flap-like outgrowth

of the antero-external edge (Plate 11. fig. 1, *k*) is very constant in its occurrence; and this also is not unrepresented in the genus *Rana*.

The hyoid arch consists of three elements—two large massive lateral cartilages or ceratohyals (fig. 1, *ch.*), which later will form the anterior cornua of the hyoid apparatus, and a small median cartilage or basihyal (*bh.*). There are thus in the hyo-branchial skeleton at this period five distinct and separable cartilages, as has been held to be the case in the tadpole of the common frog from the time of Cuvier (8) onwards. Gaupp states (14. p. 433) that in *Rana fusca* tadpoles the whole cartilage is continuous, without fibrous tissue intervening. I have not been able to procure tadpoles of this species; but I have made a careful examination of tadpoles of suitable age of *Rana esculenta* and *R. temporaria*, and in both of these the five cartilages are very sharply defined. I am inclined to think that the imperfections of the method adopted by Gaupp are largely responsible for his departure from the generally accepted view. As mentioned above, it is very difficult to discriminate between embryonic cartilage and fibrous tissue by their histological characters.

The ceratohyal or lateral hyoid bar is a stout massive cartilage closely wedged in between the branchial cartilage behind and the meckelian cartilage in front. The posterior edge is hollowed out superiorly so as to allow the anterior pointed extremity of the branchial basket to overlap it. The anterior edge of the cerato-hyal is thin, and runs parallel with the attenuated mandible, almost in contact with it. The distance between the outer extremities of the hyoid arch is considerably less than the maximum diameter across the branchial skeleton. The two ceratohyals touch one another in front; but the posteriorly directed processes of their median ends are separated by the basihyal, and are wedged in between the divaricated ends of the branchial skeleton. The basihyal is cuneiform and pointed anteriorly. Its posterior surface is applied to the branchial cartilage immediately in front of the thyroid bodies *. I regard this median cartilage as the basihyal because of its intimate relation to the ceratohyals; but I am quite prepared to agree with Parker (34) that when, as in *Alytes*, six elements instead of five are present in the larval hyobranchial skeleton, the extra

* I am at a loss to understand why Parker (33. Pl. 58. fig. 3, *tr.g.*) figures the "thyroid glands" close up under the auditory capsule.

small cartilage between the ceratohyals is undoubtedly the basihyal, and that the larger, and more posterior, unpaired cartilage, which is of more constant occurrence, has rather the value of a basibranchial. Schulze (38) still holds to the original view of Dugès (10), that this latter is the basihyal (basihyoid).

The larynx at this stage is quite diminutive in size, and lies above the level of the internal reflected margins of the branchial cartilages. The width of the larynx is hardly more than that of one of the bronchi, and the length of the glottis is about half the width of the larynx. The bronchus is not sharply marked off from the lung, but appears rather as a tubular non-sacculated continuation of it. The bronchus and lung are about equal in length. As might be expected at this early stage, the lungs are very small, and the total length of bronchus and lung together is not more than the maximum transverse diameter of the branchial skeleton. Arising from the dorsal surface of the anterior end of each bronchus is a curious thin-walled sac (Plate 11. fig. 1, *p*) which runs up laterally to the œsophagus, and is lodged beneath the ribs (see p. 120) of the anterior vertebræ. The significance of these sacs it is difficult to estimate: they are probably to be regarded as accessory lobes of the lung, since their walls so closely resemble the lung-tissue. They are present in all the larvæ of *Xenopus* that I have examined, but are altogether absent in the adult. I have found nothing to correspond with them in either the young or adult of *Pipa*.

Stage II. (Plate 11, fig. 2.) *Tadpoles with fore limbs moderately well developed, pigmented, but not markedly angulate.*

By comparison with Stage I., the most important difference to be noted in Stage II. is the reduction in size of the branchial skeleton. The hyoid arch and mandible show no great change. The curvature of the outline in the dorsal view of the branchial skeleton is no longer seen, but each half is roughly five-sided. The inflation is less conspicuous, and the basket is considerably shallower. The overhanging fold at the anterior end is missing, although the ledge projecting outwards from the applied mesial surfaces still remains. The branchial clefts have not altered; and they serve to show that the absorption has been greatest anteriorly. The first branchial arch (Pl. 11. fig. 2, *cb.* 1), which before fitted so closely into the concavity at the back of the ceratohyal, now barely overlaps the ventral ledge of that cartilage

The ceratohyal has not shared in this modification, and so a vacuity now exists between its outer end and the branchial skeleton. The anterior portion of the basihyal has been absorbed, and a cleft is beginning to appear between the median extremities of the ceratohyals. The distance between the outer ends of the ceratohyals is now slightly less than the maximum transverse diameter of the branchial skeleton. The larynx, bronchi, accessory pulmonary lobes, and the lungs are all larger than before, but are not otherwise noteworthy.

STAGE III. (Plate 11. fig. 3.) *Tadpoles with well-developed fore limbs, sharply bent. Absorption of the tail not yet commenced.*

Considerable changes have taken place in the hyobranchial skeleton since Stage II., far more than would be suspected from a superficial examination of the tadpoles. The five cartilages to be seen in Stages I. and II are no longer distinguishable. The basihyal has either been absorbed, or has fused up with the neighbouring cartilages in such a way as to leave a deep cleft, enlarging posteriorly between the median ends of the ceratohyals. The posterior end of this cleft marks the position of the future hyoglossal foramen; and it only requires a further enlargement of the cleft, accompanied by a secondary union of the ceratohyal cartilages in front, to bring about the adult relations. It is a matter of the keenest regret that I am unable, from lack of material, to add a circumstantial account of these later changes.

The mandible and ceratohyal have changed but little; and the concavity at the back of the latter, vacated by the first branchial arch, still remains. The branchial skeleton, on the other hand, has been considerably reduced. The first branchial arch is now no thicker than the second, and a wide space intervenes between it and the ceratohyal. All trace of inflation has disappeared, and the flattened branchial apparatus bears a much closer resemblance to that of the common frog than it did before. The three branchial clefts have not altered except in size, and, judging by analogy with tadpoles of other species of Anura, they will not do so. The arches will be absorbed, and the clefts will disappear in consequence; but the latter will play only a passive part in the change. The distance across the branchial skeleton is now considerably less than the extreme width of the hyoid arch. That the absorption of the branchial skeleton has been a marginal one is seen by the fact that in the first stage the external edge of the

branchial basket-work fits underneath the auditory capsule so closely that considerable care is required to separate the two; but in this third stage the whole of the branchial skeleton lies in the floor of the pharynx.

The most interesting feature of this stage is the formation of the thyrohyals, which may be seen arising from the hind edge of the median basal plate of cartilage, as a paired outgrowth perfectly independent of the four branchial arches (Pl. 11. fig. 3, *t*). This is universally accepted as the mode of origin of the thyrohyals in the tongued Anura. It was clearly set forth in the works of Cuvier (8), St.-Ange (36), and Dugès (10), was confirmed by Parker (32) in his exhaustive treatise on the development of the skull of the common frog, and has recently been corroborated by Schulze (33) and Gaupp (14). These thyrohyals as yet show no trace of ossification, and are quite free from the laryngeal skeleton. Here, then, is conclusive evidence of the secondary nature of that connexion between the hyobranchial and the laryngeal skeleton, which distinguishes the Aglossa from all other Amphibia. The fourth branchial arch has shrunk considerably since Stage II., especially towards its median end, so that not only is it now no thicker than the third arch; but it no longer underlies the larynx. In fact, although the larynx has not shifted in position relatively to the branchial clefts, there has appeared a space between the fourth branchial arch and the larynx. Into this space the thyrohyals grow.

Owing to paucity of material I have been unable to determine the mode of origin of the great alæ of the adult hyobranchial skeleton; but it is highly probable that, as in *Pipa*, these are the result of secondary outgrowths from the undivided hypobranchial part of the branchial skeleton (Pl. 11. fig. 3, *hb*), and not, as might be suggested by a comparison of fig. 3, Pl. 11. and fig. 1, Pl. 8, of the persistence of such part of the branchial skeleton as still remains, under a condition of closure of the clefts. The ceratohyals, still massive, are fated to undergo a certain amount of absorption. The absorption, however, is not excessive, and the lamellar expansions of cartilage on the internal and external edges of the anterior cornua of the adult clearly owe their presence to the fact that the absorption of cartilage is less complete than in most Anura. The laryngeal skeleton has altered but little since Stage II. The arytenoid cartilages (Pl. 11. fig. 10, *ar.*) are very large in proportion. They

resemble in shape the arytenoids of most Anura (cf. *Bombinator*, fig. 13), and differ in a marked degree from the arytenoids of the adult. They are closely applied to one another in the median line, as in the typical Anuran larynx, and not as in the adult *Xenopus*. The cricoid is an annular cartilage, more extensive on the ventral than the dorsal surface, and quite free from the thyrohyals. The ventral portion terminates anteriorly in a blunt point a short distance behind the anterior ends of the arytenoids, and is produced behind into a pair of narrow bands (fig. 10, *br.*) which support the ventro-internal walls of the bronchial tubes. This early appearance of the bronchial cartilages is well worthy of note. The roof of the larynx is expanded in front, and the dorso-lateral corners are produced into a pair of blunt processes which are doubtless to be identified with the blinker-shaped processes of the adult (Pl. 8. fig. 3, *bl.*). The posterior edge of the roof is concave. The sides of the cricoid do not extend forward, so that the whole of the arytenoid can be seen in a side view.

Parker neither discusses nor figures the branchial skeleton of his youngest *Xenopus* larva—first stage, with no traces of paired limbs, total length 1¼ inch—but the figure he gives (33. Pl. 56. fig. 6) of the hyoid arch and mandible of this stage corresponds almost exactly with that of my Stage I. The broadened posterior extremity of the basihyal he regards as the first basibranchial, but beyond that we do not differ. Parker's second stage—tadpole, 1⅜ inch long—of the limbs of which we have no means of judging, would also appear to correspond with my first stage; for in his side view of the hyobranchial skeleton (which, curiously enough, he draws upside down), the branchial cartilage is still considerably inflated and fits up closely behind the ceratohyal. He is silent concerning the hyobranchial skeleton of his third stage,—tadpoles at their largest size—; but in his fourth stage—young, with large legs and diminishing tail—which, judging from the second qualification, should be older than my Stage III., he figures (33. Pl. 58. fig. 4) the two ceratohyals as still distinct, and the basihyal as still recognizable. The cartilage, which in this figure he indicates by outline only and marks *br.* 1, is, I am convinced, the whole of the hypobranchial plate, shown in my fig. 3 at *hb.*

Pipa americana.

Here, as in *Xenopus*, the mode of development of the hyobranchial skeleton is practically unknown. Parker has contributed a certain amount of information*, but beyond this the subject has not been touched. Grönberg (18. p. 635) speaks of having discovered in the larva of *Pipa* that, as in the adult female, the isthmus between the anterior and the posterior parts of the basal plate is a continuous cartilage, but he gives no further information, nor any figures of larval structures. The specimens available for this part of the investigation were sufficiently plentiful to render it possible to obtain much more complete and satisfactory results than was the case with *Xenopus*. For many of the specimens I am indebted to the kindness of Prof. G. B. Howes; the remainder were obtained by purchase from V. Frič of Prague.

It will be found convenient to choose six stages of development for description here. There is more uniformity in the size of embryos of the same age than in *Xenopus*, since the young of

Embryos of Pipa.

Measurements in millimetres.

	From snout to root of tail.	Length of tail.	Length of extended hind limb.	Length of extended fore limb.
Stage I.	10	12	4	0
Stage II............	12	11	6	3
Stage III.	11·5	6·5	7·5	5
	13	8·5	7	5
	12	10	7	5
Stage IV.	11	9	7·5	4·5
	11·5	10	7	4·5
	9	10	8	4·5
	12	6	7·5	4·5
Stage V.	11	9	9	5
	11	9·5	10	5
Stage VI.	14	0	10	5·5
	13·5	0	11	5·5
	15	0	11	8
	13	3	10	6
	14	0	10·5	5·5

* For a criticism of which, see p. 110.

Pipa are less dependent on external conditions, being provided at the outset with a large quantity of food-yolk, and being lodged during their development in the integumentary pits on the back of the mother. But it happens unfortunately that very little idea of the extent of development of the hyobranchial skeleton can be obtained from an examination of the external features, and it is consequently necessary in most cases to dissect out this portion of its body before deciding what stage any particular embryo has reached. The table on p. 102, compiled from the *Pipa* embryos examined, will show how useless actual measurements are for discriminating the various stages. Stage I. is distinguished by the fact that the fore limbs are not yet extruded, and Stage VI. is marked by the complete absorption of the tail; but there is no safe guide for distinguishing the intermediate stages.

STAGE I. (Pl. 11. fig. 4.) *Embryo with abdomen much distended by unabsorbed yolk. Fore limbs not yet extruded. Length of body* 10 *mm., tail* 12 *mm.*

I have called this Stage I. because it is the youngest that I have been able to examine; it is, however, highly probable that the hyobranchial skeleton of younger embryos would show many features of interest. Owing to the fact that the larvæ of *Xenopus* are freely-swimming tadpoles, while the young of *Pipa* only quit the integumentary pits on the back of the mother after their metamorphosis is complete, it is no easy matter to correlate the stages of development in the two genera; but, judging from the extent of development of the hyobranchial skeleton alone, this first stage of *Pipa* would seem to be equivalent to a stage intermediate between those numbered II. and III. in *Xenopus*. The branchial arches are rods of cartilage and not sheets, as in the early stages of *Xenopus*, and the lines of demarcation of the five elements of the larval hyobranchial skeleton are not to be distinguished. The hyobranchial skeleton is one continuous cartilage, considerably broader across the branchial than across the hyoid region. The branchial skeleton has the appearance of having already suffered considerable absorption. The larynx lies in the deep indentation in the middle of the posterior border, and does not overlie the branchial cartilage. The three branchial clefts are approximately equal in length, but in width the posterior has the advantage. The first branchial arch is separated

from the hyoid by a distance equal to its own width; and the breadth of the cartilage connecting the hyoid and branchial divisions of the hyobranchial skeleton is nearly equal to the antero-posterior diameter of the median basal plate, from which latter the four great lobes, two hyoid and two branchial, radiate.

The hyoid cornua are large, and each in shape resembles an axe-head. The antero-external convex edge is thin and shows signs of absorption. It is important to note that, although the external or lateral extremities of the mandible and ceratohyal are nearly in contact, a considerable space is enclosed between their more median parts, and these relations are maintained as long as the ceratohyal is recognizable. In *Xenopus*, it will be remembered, the median ends of the ceratohyals lie close up behind the mandible. Although the hyobranchial skeleton of the early *Pipa* embryo exhibits the aforementioned peculiarities, it is nevertheless far less aberrant than that of the *Xenopus* larva.

Parker states (33. p. 649) that there are neither external nor internal gills in the embryos of *Pipa*, but it is evident that he had never seen Wyman's paper describing (44. p. 371) the existence of three pairs of external gills, internal gills, and a pair of branchial clefts. It would be difficult to believe that a hyobranchial skeleton, conforming so closely to the normal anuran type as does that of the present stage, should not be associated with branchiæ of some sort.

STAGE II. (Pl. 11. fig. 5.) *Embryo with abdomen not distended by yolk, although on dissection much is found still unabsorbed. Hind limbs flexed,* 6 *mm. in length when straightened out. Fore limbs* 3 *mm. Length of body* 12 *mm., tail* 11 *mm.*

This stage does not differ to any great extent from the first, and is not so strictly intermediate between Stages I. and III. as could be wished; but here again the deficiency is to be accounted for by the difficulty of obtaining embryos of any particular age. The chief difference between this and the preceding stage is to be noted in the hyoid arch. Considerable absorption has taken place—a significant foreshadowing of the later complete disappearance of this arch. The erosion is greatest anteriorly, so that the antero-external edge, before convex, is now concave, while the anterior indentation between the two cornua has broadened out. Since no absorption yet

takes place at the free extremities of the cornua, there is no diminution in the total width of the hyoid skeleton. The most important change which has taken place in the branchial skeleton is the severing of the commissural or epibranchial cartilage between the lateral extremities of the first and second branchial arches. An indication of this is to be seen in Parker's figure (33. Pl. 63. fig. 4) of a stage much earlier than this. It is interesting as being the first step in the total disintegration of the branchial arches which so soon supervenes. The larynx has advanced in position so that it is now in contact with the branchial skeleton.

Stage III. (Pl. 11. fig. 6.)

It is impossible to give a diagnosis of embryos of this and the two following stages, as a glance at the table of measurements will show. The changes in the hyobranchial skeleton at this period appear to be unaccompanied by any marked alteration in the external appearance of the embryo.

The general aspect of the hyobranchial skeleton is now entirely changed, and the absorption of cartilage is proceeding rapidly. The hyoid cornua are reduced to rods of cartilage, while the branchial arches are breaking up, chiefly at their peripheral ends. Before proceeding to a detailed description of the skeleton at this stage, it may be well to point out that in *Xenopus* the hyoid arch remains practically unchanged during the time that the branchial arches are undergoing their gradual reduction, but that in the early stages of *Pipa* it becomes rapidly diminished and the branchial skeleton follows but slowly. At Stages III. and IV. of *Pipa* the rapid absorption of the branchial arches begins, and then it is a race, as it were, between the hyoid and branchial arches for first disappearance. The rate of absorption at this period is excessive, so much so that embryos the hyobranchial skeleton of which has reached Stages III. and IV., and even V., are externally indistinguishable: in other words, that the rate of change in the hyobranchial apparatus exceeds by a good deal that of the general metamorphic changes of the body.

In this Stage III. the diameter across the branchial skeleton is not greater than that across the hyoid arch. This may be partly due to an elongation of the hyoid cornua; but the more important factor in this change of proportion is undoubtedly a *shrinkage* of the branchial arches. This is indicated to some

extent by the shortening of the branchial clefts before they become broken open peripherally; but it is more conclusively shown by the fact that, while in Stages I. and II. the aortic vessels made up of the four efferent branchial arteries run alongside the commissural or epibranchial cartilages that connect the outer ends of the branchial arches, there exists in Stage III. a considerable interval between the paired aorta and such parts of the commissural cartilages as yet remain. This is not to be explained by a widening or separation of the aortæ, for the actual length of the branchial vessels has not increased. The commissure between the first two arches was already ruptured in Stage II.: it has now completely disappeared. The second commissural cartilage has severed its connexion with the second branchial arch, but remains attached to the third. The third commissure is still intact. The first branchial arch is undergoing reduction at its proximal as well as at its distal extremity. The cartilage at the junction of the first ceratobranchial and the hypobranchial plate (Pl. 11. fig. 6, †) is very thin, and showed in two of the specimens examined a distinct indentation in the edge,—a foreshadowing of the dismemberment of the arch which is completed in Stage IV. A considerable reduction is to be noticed in thickness of the second branchial arch. The fourth arch, on the contrary, is thicker than before, especially towards its proximal extremity, where it is in continuity with the hypobranchial plate. The latter plate has become perforated by a paired foramen (*t'*) lying immediately over the thyroid bodies. The cartilage situated to the outer side of the foramina shows unmistakable signs of absorption, but the front and hind portions of the hypobranchial plate are increasing in thickness.

The thickening at the posterior edge of the plate is highly important, because, as will be seen by comparison with the later stages, it indicates the formation of the thyrohyals. The thyrohyals in *Pipa* do not grow out as distinct processes as they do in the tongued Anura, and even in *Xenopus*, but are formed by an addition of cartilage to the hind edge of the hypobranchial plate. The added cartilage also extends outwards behind the proximal end of the fourth branchial arch, and this it is that causes the apparent increase in thickness of the last arch. There is no augmentation of the cartilage of the arch, but an addition to its posterior edge. This is indeed a most aberrant mode of formation of the thyrohyals, unparalleled in the Anura; but the

development conforms to the general rule in so far that the thyrohyals arise from the hinder part of the hypobranchial plate, and at the proximal end of the fourth branchial arch.

The thickening of the anterior portion of the hypobranchial plate is the developing ala of the hyobranchial skeleton of the adult. It is situated, strictly speaking, anteriorly to the level of the first branchial arch, from which it is already beginning to separate by the formation of the notch shown at † in fig. 6. The bar of cartilage lying in the median line between the two foramina will become the isthmus (Pl. 9. fig. 1, *i*) which connects the anterior and the posterior or laryngeal parts of the basal plate of the adult. The hyoid cornua or ceratohyals are much thinner than in Stage II. and are slightly longer. They are of approximately uniform thickness all along, except at their median extremities, where they are reduced. They are delicately curved, the anterior margin being convex and the posterior concave. The space between the hyoid and first branchial arches has increased in size, and the indentation between the two hyoidean cornua is no longer V-shaped but semicircular, with a slight tendency to squareness. The larynx, which has increased but little in size, now overlaps the developing thyrohyals *.

Stage IV. (Pl. 11. fig. 7.)

The difficulty experienced in dissecting out the branchial arches in the last stage, owing to the looseness and softness of the disintegrating cartilage, here reaches a maximum; and it is only with the very greatest care that the arches can be recognized at all. All four have severed their connexion with the hypobranchial cartilage, and the epibranchial or commissural cartilages at their distal ends have completely disappeared. The part of the hypobranchial cartilage postero-external to the thyroid foramen and between the developing ala and thyrohyal is not yet entirely absorbed, but the tissue in this position is of a very loose character. The most instructive lesson that this stage teaches is that the ala of the adult skeleton is a purely hypobranchial derivative and that it is morphologically anterior to the first branchial arch. Parker's interpretation, therefore, of the ala as the confluent first and second branchial arches of the larval skeleton is no longer tenable.

* In order to avoid confusion, it has been omitted in figs. 6, 7, and 8; its position in fig. 9 is indicated by the dotted line.

In the hyoid arch the absorption has been greatest towards the median extremity, so that the cornua taper inwards to a point which is still connected by a very ill-defined tissue with the axial structures. A new cartilage, as yet but faintly outlined, is appearing between the inner ends of the hyoid cornua, and tends to convert the notch or indentation at the front of the hyobranchial apparatus into a foramen. The larynx now completely overlies the developing thyrohyals, and its most anterior point is situated exactly over the middle of the median bar or isthmus between the thyroid foramina.

Stage V. (Pl. 11. fig. 8.)

The ceratobranchials have completely disappeared at this stage, and the thyroid foramina have been converted into deep clefts between the alæ in front and the thyrohyals behind. Both alæ and thyrohyals are now sharply outlined, and the whole apparatus has begun to assume the peculiar aspect of the hyobranchial skeleton of the adult. The alæ are racket-shaped. The hyoglossal notch has been converted into a complete foramen (fig. 8, *h*) by a further development of the cartilage which in Stage IV. was beginning to make its appearance between the median ends of the hyoid cornua. The new cartilage has assumed a definite outline and tapers anteriorly to a blunt point. The ceratohyals themselves are only to be recognized as vestigial cartilages, blunt externally and pointed at their inner ends, situated behind and internal to the articular end of Meckel's cartilage. It is here worthy of remark that the absorption of the hyoid cornua has proceeded in a most regular manner from the median end outwards, the last remnant to disappear being the external extremity. There is nothing to be recorded with regard to the laryngeal skeleton except that it has been gradually increasing in size, and that its diameter is now as great as the distance between the centres of the alary cartilages.

Stage VI. (Pl. 11. fig. 9.) *Embryos with no tail, or with the merest remnant of it. Length of body about* 14 *mm. Length of hind limb when extended* 10 *or* 11 *mm. Fore limb* 6 *mm.*

Although the embryos at this stage are still comfortably ensconced in the maternal integumentary pits, the hyobranchial skeleton does not differ materially from that of the fully-grown adult, the most important differences being that the thyrohyal is

unossified and still readily separable from the larynx proper. The thyrohyals have increased in length so that their extremities can be seen projecting beyond the sides of the larynx. Their extremities have also become dilated. The alæ have enlarged very considerably, and the maximum transverse diameter of the hyobranchial skeleton is now three times the width of the larynx. The backward growth of the alæ is even more remarkable than their increase in width. The line joining the extremities of the thyrohyals passed behind the alæ in Stage V., with a considerable distance to spare. In the present case it passes approximately through the centres of the now oval alary plates.

The hyoglossal foramen is nearly circular in shape and is much smaller than before. The cartilage bounding the foramen has been greatly reduced in thickness, and the anterior tapering process (Pl. 11. fig. 9, *ch'*.) is now as sharply pointed as in the adult. The larynx is still remarkably different from that of the adult. This is a noteworthy fact, because Wilder (42. p. 306) states that in *Rana* tadpoles, the caudal stump of which has not yet disappeared, the larynx is practically in the adult condition. No peculiarities which might be attributed to sexual differences were to be seen in the larynx of any of the specimens examined. Since, however, the reproductive organs were not sufficiently advanced to enable me to determine the sex, it was not to be expected that any of the secondary sexual characters should be recognizable.

The arytenoid cartilages have the form which obtains in most adult Anura; they are pointed in front and are closely applied to one another by their thin dorsal borders. Their broad posterior ends fit closely into the ring of the cricoid cartilage, the ventral portion of which is produced forwards to furnish additional support (see figs. 11 and 12). The dorsal portion of the cricoid ring has the form of a band running transversely, and both anterior and posterior edges are nearly straight. The sides are more extensive than in *Xenopus* Stage III. (see fig. 10), and the floor, which is roughly triangular in shape, is deeply incised behind. A comparison between this embryonic larynx and the adult larynx of *Bombinator* (fig. 13) is very instructive. The bronchial processes (*br.*) of the latter are not represented, and the roof of the cricoid is not so expanded, but otherwise the resemblance is very close. The ventral position of the thyrohyals with regard to the larynx in *Pipa* is of course exceptional.

It has been brought about, not by the approximation of the thyrohyals towards the median line, but by the forward migration of the larynx over the hinder part of the hyobranchial skeleton. The membranous space in the floor of the larynx in the adult female (Pl. 9. fig. 1) has evidently arisen by the absorption of cartilage, for it is not represented in any of the young stages. In this, as in the five preceding stages, the lungs exhibit the accessory lobe on the mesial surface, which is such a distinguishing feature of the lungs of the adult *Pipa*. The bronchi are still short,—a matter of some importance, since in *Xenopus* the bronchus is nearly as long as the lung itself even in the earliest stage.

Parker includes, in his first stage of *Pipa*, embryos from the dorsal pouches, of a total length of 9 lines, apportioned as follows:—head 2, body 3, tail 4. The external appearance of the embryo (33. Pl. 60. figs. 1 and 2) would show that this stage is earlier than my first stage, since the body is very small in proportion to the size of the yolk-sac. But, judging by the figure of the hyobranchial skeleton (33. Pl. 60. fig. 4), it should be later, for both hyoidean and branchial plates are represented as less expanded than in my Stage I. Parker figures the hyoid portion of the hyobranchial skeleton as distinct from the branchial, the right and left halves of each portion being united across the median line. These confusing characters render a more exact correlation of the stages impossible. Parker's second stage—ripe young, 6½ to 7½ lines in length, no tail—is older than my Stage VI., and the hyobranchial skeleton does not differ materially from that of the adult, except that the thyrohyal is unossified. Parker states (p. 655) that the ceratohyal has disappeared, and indicates by a dotted line the position which it should occupy; but, since he records no stage intermediate between that at which the hyoid is "at its maximum" (p. 652) and that at which it has entirely disappeared, he cannot be said to have unequivocally proved the absorption. He mistakes the floor of the larynx for an expansion of the hyobranchial cartilage and calls it the second basibranchial; and he fails to differentiate the thyrohyal from the laryngeal cartilage, although the two are readily separable at this age. The ala of the adult hyobranchial skeleton he regards as a derivative of the first and second branchial arches, the thyrohyal

of the third and fourth, and the hyoglossal foramen as a secondary fenestration in the basibranchial cartilage. In none of these respects do my observations accord with his.

General Conclusions, and Discussion of the Affinities of the Aglossa.

The most important outcome of the study of the development of the hyobranchial skeleton which forms the subject of the preceding section is the demonstration of the fact that the wings of the adult skeleton cannot be regarded as the derivatives of any particular branchial arches, any more than can the two lateral processes of the body of the hyoid, lying between the anterior cornu and the thyrohyal, in the frog, which, as Gaupp (14) has so admirably shown, are developing independently, while the branchial arches are becoming absorbed. There is, it is true, a great temptation to homologize processes and projections of adult skeletal parts with structures of larval significance, but it is only by resisting the temptation that a due regard for observed fact can be assured. Careful inspection of the evidence upon which Parker bases his deductions shows it to be of the most scanty description, and discloses the fact that the homology he establishes between the alæ and the first two branchial arches, and between the thyrohyals and the third and fourth, is conjecture rather than a legitimate conclusion based upon the information in his possession. Cope does not accept Parker's interpretation of these structures, but it is extremely difficult to discover what his own views really are, for while he copies (7. Pl. 76. fig. 1) Parker's figure of the hyobranchial skeleton of *Xenopus* (33. Pl. 58. fig. 5), and marks the wings *cb.* 1 and the thyrohyals *cb.* 2, yet on p. 252 he states that the Aglossa have the *third* ceratobranchials greatly elongated,—and this in spite of his generalization (p. 234) that the thyrohyal of Salientia is the *fourth* ceratobranchial. The relations of the geniohyoid muscle point in the direction of the alæ being homologous with the lateral cartilages in front of the thyrohyal (processus postero-lateralis, Gaupp, 14) which attain such an exceptional length in *Bombinator*, *Pelobates*, and *Pelodytes*. The anterior position, however, which the alæ occupy during development rather shakes one's faith in this determination.

The morphological significance of the thyrohyals in Anura

generally is a question which cannot be regarded as definitely settled. That they are only *physiologically* equivalent to the mammalian thyrohyals, which they so closely resemble, is tolerably certain. The thyrohyals are derived from the branchial skeleton in both, but from parts which are not homologous. The view propounded more than seventy years ago by Meckel (**27**. p. 240) and Cuvier (**8**. p. 397), that the thyrohyals of Anura represent the fifth ceratobranchials of Elasmobranch fishes and the lower pharyngeal bones of Teleosteans, is well worthy of mature consideration; and it may be a not unimportant fact that the fifth ceratobranchials are so much more strongly developed than the preceding four in most Rays and Teleosteans. When, later, the study of development disclosed the exceptional mode of origin of the Amphibian thyrohyals, authors became silent concerning their morphological value, and simply described them as outgrowths of the hypobranchial plate of the tadpole, behind the fourth branchial arch. More recently Parker (**35**. p. 173, and **34**), who was never at a loss for a working hypothesis, regarded them as the fourth ceratobranchials, and in this he has been followed by Walter (**40**) and others.

The fact of the thyrohyals arising so late and as outgrowths from the hypobranchial plate, and not, like the branchial arches, by differentiation of the cartilage, does not, however, appear to me to militate seriously against our regarding them as the fifth ceratobranchials. Their late development is certainly connected in some degree with their relation to the larynx, which, like the rest of the pulmonary respiratory system, does not attain any considerable development until branchial respiration is waning. Given five branchial arches, four of which are connected with branchial respiration and the fifth with pulmonary respiration, and considering that respiration is at first branchial and later pulmonary, it is in strict accord with such laws as we have been able to formulate concerning the development of structures not required for use simultaneously, that the fifth arch will not develop until it is wanted; and then, as is the case with most organs the development of which is delayed, it will be formed rapidly, and most probably in an exceptional manner. Similar instances of accelerated and abbreviated development of organs, the appearance of which has been delayed, may be seen in the formation of the mesonephros of the frog from a blastema instead of by peritoneal tubules, in consequence of the pro-

nephros subserving all the requirements of the tadpole until a late larval stage; and the direct development of the first three pairs of appendages in those Crustacea in which the Nauplius stage is suppressed,—the metamorphosis of the larval appendages is omitted, and when the appendages appear they assume directly the form of the antennule, antenna, and mandible of the adult. On this hypothesis the difference in the mode of origin of the thyrohyals in *Xenopus* and *Pipa* is probably not morphologically important.

In 1881 Parker (34) propounded the view that the four pairs of irregular cartilages (Spicula, Gaupp, 14) at the junction of the branchial arches with the hypobranchial plate in the tadpole were the true ceratobranchials of the fish, and that the arches themselves were but extrabranchials,—accessory structures peculiar to the tadpole of Anura and not represented in the larvæ of Urodela. Also, that the fourth pair of these processes became the thyrohyals. This view, although entertained in some degree by Cope * (7. p. 244) and Schulze (38. p. 12), cannot be substantiated by the facts of anatomy and development. Gaupp (14. p. 414) forcibly describes it as "ganz absurd," and other writers, such as Stöhr (39) and Naue (31), still adhere to the earlier interpretation. The relation of the vascular tissue to the supporting cartilage in a tadpole is certainly exceptional, but this is due to the enormous size of the pharyngeal cavity and the thinness of its lateral perforated walls. The main branchial blood-vessels lie external to the cartilage in both tadpole and fish, whereas if the spicula are the true arches and the branchialia something external to them, the vessels should run upwards from the spicula to the roof of the pharynx. As it is, even the paired aorta lies external to the branchialia of the tadpole.

Marshall (24. p. 164) describes a pair of diverticula in the floor of the pharynx, behind the last gill-clefts in *Rana* tadpoles, which disappear after the metamorphosis, and he takes them to represent in a modified form a fifth pair of branchial clefts. He does not explain their relations to the thyrohyals, but since he says the pits are situated at the sides of the glottis it is evident that they are in their immediate vicinity. The presence of anything that can be regarded as the fifth branchial cleft lends support to the hypothesis that the fifth branchial arch is also represented.

* Cope, however, contradicts himself by regarding the arches in Pl. 50. fig. 2 as ceratobranchials.

With regard to the arytenoid cartilages, authorities are all agreed that they are the most anterior segments of the tracheal skeleton: the point of dispute concerns the origin of the latter. Recent literature (Gegenbaur 15, Göppert 16, Wilder 41 and 42) shows that there is a rapidly growing tendency to regard all tracheal, bronchial, and arytenoid cartilages in Amphibia as products of the segmentation of a pair of elongated cartilages—the fifth branchial arches—extending primarily along the right and left sides of the trachea. The determination turns chiefly upon the arrangement of these lateral cartilages in the lower Urodela; but it must not be forgotten that in these we are dealing with long-bodied animals in which the length of trachea is evidently correlated with that of the body: that is to say, that the organ under consideration is not in its most primitive condition. The subject is far too extensive to discuss in the limits of these pages, but, in the case of Anura, there appears to me to be far more to recommend the homology of the fifth branchial arch of the fish with the thyrohyal than with the arytenoid and cricoid cartilages.

I regard the laryngeal cartilage of the frog as the perfect equivalent of the cricoid cartilage of mammals, and I do not see the force of Wilder's argument (42. p. 285) for calling it the "annulus;" for, admitting that thyroid cartilages of whatever form are secondary * hyobranchial derivatives, and that the cricoid cartilage is formed by the modification of the first one or more tracheal rings, there is sufficient differentiation of laryngeal structures here for all practical purposes. If the word "cricoid" be employed in a strict sense, we should have to confine its application to mammals, and to invent new names for the chief laryngeal cartilage in other air-breathing vertebrates, according to the amount of tracheal cartilage involved.

With the thyroid cartilage the case is different, and the term must be employed more cautiously or hopeless confusion will result. Grönberg, for instance, says with regard to the floor of the larynx of *Pipa* (18. p. 635):—"Wenn Dubois' Anschauung richtig ist, dass die Cartilago thyreoidea bei den Säugethieren aus dem 4. und 5. Visceralbogen nebst zugehöriger Copula hervorgegangen ist, so können wir hier zum ersten Mal im

* I use the word advisedly, in view of the prevailing custom, just cited, of regarding the whole of the respiratory cartilages as primary branchial derivatives.

Thierreich von einer Cartilago thyreoidea im Sinne des Säugethierschildknorpels sprechen." But, as already objected by Wilder (42. p. 291), if we apply the term "thyroid" to products of the fourth and fifth visceral arches (*i. e.* the second and third branchial arches), we must certainly not employ the same word for structures developed *behind the fourth branchial arch*, although perhaps the two may be physiologically identical. Mayer (25. p. 541) had previously applied the term "os thyreoideum" to the anterior part of the floor of the larynx of *Pipa* (not the whole of it, as Grönberg appears to intimate), but he probably did not intend the comparison to be taken too strictly. It is sufficiently misleading to employ the same word thyrohyal in Anura and Mammalia for structures only functionally similar; but custom has so familiarized us with the enormity that we have come to associate different morphological ideas with the word according to the animals to which it is applied. Still, this fact does not warrant the introduction into an already too involved literature of fresh sources of confusion.

It were rash to institute, as many do, a system of classification based on the characters of a single organ, or even a few associated organs; but since the systematist has recourse to as many structural differences and resemblances as are within his knowledge when drawing up a scheme of classification, it may be well to ascertain what weight may be allowed to the various details set forth in the preceding pages when applied to the solution of the problem of natural affinity. Both *Xenopus* and *Pipa* have elongated bronchi, which are absent in all Phaneroglossa; but it is somewhat doubtful whether the bronchial cartilages supporting them have not originated independently in the two genera (see p. 71). The curious lobe of the lung arising from the dorsal surface of the anterior end of the bronchus in the larval *Xenopus* is not represented in *Pipa*; on the other hand, the outgrowth or lobe on the mesial surface of the lung of *Pipa* finds no counterpart in *Xenopus*. With regard to the larynx, a greater difference exists between this organ in the male and female of *Pipa* than in the females of *Pipa* and *Xenopus*. In the male of both genera the laryngeal complex is connected by ligament with the bulk of the hyobranchial skeleton; but, since these ligaments do not correspond morphologically, it is evident that we are dealing here with nothing more than an adaptation to subserve

some physiological purpose, probably to give the larynx greater freedom of motion.

Both *Xenopus* and *Pipa* have, it is true, no tongue, but is it not just possible that there is some physiological connexion between the absence of tongue, the union of the eustachian recesses into a median ostium pharyngeum, the excessive development of the hyobranchial wings, the formation of a hyoglossal foramen, the elongation of the bronchi, the absence of vocal cords, the enlargement of the larynx, and its support by the hinder part of the branchial skeleton? Admitting that the same conditions acting independently on the two genera may have resulted in the loss of the tongue or some other of the above specified peculiarities, it is quite comprehensible that the other modifications have followed as concomitant variations. The similarity of the hyobranchial and laryngeal skeleton, so far as I am aware, has not yet been employed as one of the characters pointing to a natural affinity between *Xenopus* and *Pipa*; but were the attention of the systematist directed to this feature, he would probably interpret it as corroborative detail, whereas if, as above suggested, it is physiologically related to the suppression of the tongue, he would be doubling or perhaps trebling the importance of the aglossal character, and would not be adducing new evidence. It may, in fact, be that the enlargement of the larynx as an accessory sexual organ is the primary cause of all this modification, including even the suppression of the tongue. In the Discoglossidæ and Pelobatidæ, where, as already pointed out, the larynx is much more enlarged than in most Anura, and where the tongue shows unmistakable signs of reduction, we have some such correlation as that suggested, and, what is more, a diminution of the antero-posterior diameter of the basal plate of the hyoid, coupled with a great development of the lateral outgrowths of the plate.

In *Bombinator* and *Pelobates* the mesial ends of the hyoidean cornua are connected by a dense layer of connective tissue situated below the hyoglossal muscle; and in *Pelodytes* the cornua are actually in contact in the median line, so that only a fusion of the two is required to make a perfect hyoglossal foramen. This fact is very significant, since it is only in these genera, outside the Aglossa, that any indication of a hyoglossal foramen is to be met with. The anterior cornu of *Xenopus* is broad and expansive, and thereby exhibits a retention of a

primitive condition. Similar expansions of the anterior cornua are to be seen in *Bombinator* and *Discoglossus*. The absence of the anterior cornua in *Pipa* indicates a high degree of specialization, which finds its nearest parallel in *Pelobates* * and *Pelodytes*. In the adults of these genera we have a retention of the condition seen in Stage V. in the development of *Pipa*. The greater part of the cornua are missing, but the more posterior parts have not shared in the absorption. These remnants are flat and broad in front, but are rod-like behind, where they rise up behind the auditory capsule and become attached to the skull.

The laryngeal muscular anatomy, more especially the exceptional relations of the hyoglossus and petrohyoideus of *Pipa* and *Xenopus*, would seem to indicate a close affinity between the two genera; but, on the other hand, it must not be lost sight of that these relations are correlated with skeletal resemblances, and care must be exercised not to weigh the same evidence twice over. The absence in *Pipa* of the geniohyoideus internus, the posterior position of the origin of the hyoglossus, and the insertion of the laryngeal division of the obliquus internus into the roof of the larynx instead of the extremity of the thyrohyal, are differences of no slight importance, and differences, moreover, which are not connected with skeletal dissimilarity. The relations of the hyoglossus to the floor of the mouth prove, I think, most conclusively that both *Pipa* and *Xenopus* are descended from tongued forms. Both Mivart (29. p. 283) and Cope (7. p. 247) have regarded the absence of tongue as secondary, and the union of the eustachian tubes in the middle line as evidence of a higher development. The breadth of the pterygoid bones is evidently related to this second feature.

With regard to the general muscular anatomy, Beddard (2. pp. 848 and 849) has shown that *Xenopus* differs from *Rana* and resembles *Pipa* in the "enormous extension backwards of the *Latissimus dorsi*, the absence of the *Pectoro-cutaneus*, the attachment of the muscles covering the abdomen to the fascia covering the thigh, the presence of a sheet of muscle below the *Mylohyoid* which joins the *Deltoid*, and the existence of a special muscle running from the ilium to the lung and œsophagus." On the other hand, *Xenopus* differs from both *Rana* and *Pipa* in the

* Parker (34. Pl. 25. fig. 9) shows the hyoid cornua of *Pelobates* as complete, but this is a mistake.

"large size and attachment of the *Sartorius*, the single-headed *Semitendinosus*, the great extent of the *Pectoral*, which completely covers the *Sternoradialis*, and the large size of the *Glutæus*." It would be of great interest to see whether any of these nine peculiarities occur in Discoglossidæ and Pelobatidæ. The extent of development and the almost identical form of the "diaphragm," and the extension of the abdominal muscles on to the thigh in both *Xenopus* and *Pipa*, Beddard points out (2. p. 840), may possibly have arisen independently, in relation with the assumption of a purely aquatic habit, but he inclines to the belief that they are marks of real affinity. It is strange how very many of the structural peculiarities which would appear to point to a natural relationship between *Xenopus* and *Pipa* are more or less explicable as physiological adaptations.

Besides the families Xenopodidæ and Pipidæ, Cope (6. p. 99 and 7. p. 258) includes in the Aglossa a third family, the Palæobatrachidæ, represented by extinct forms only. The special interest of the third family in this connexion lies in the fact that Wolterstorff (who gives, 43. pp. 8–12, a most useful list of references to papers dealing with *Palæobatrachus*), regards the question of affinity as turning largely upon the relations of the thyrohyals to the other skeletal parts:—"Ob eine Zunge vorhanden war, weiss man noch nicht. Dies, also die Trennung von den Aglossa, müsste durch Auffindung von Zungenbeinhörnen bewiesen werden" (43. Theil i. p. 45). Wolterstorff, although admitting many points of affinity with the Aglossa, appears rather inclined to accept Boulenger's view (43. Th. ii. p. 75 (155)), that *Palæobatrachus* is most nearly allied to the Pelobatidæ among living Anura, and to the genus *Batrachopsis* in particular. Did the genus possess an ossified laryngeal skeleton intimately associated with the thyrohyals, the evidence of affinity with the Aglossa would be incontestable, for there is nothing approaching such a condition in any other Anura. On the other hand, should the hyoid apparatus prove to be free, the affinity would in no wise be disproved. A minute examination of the specimens of *Palæobatrachus* at the Natural History Museum, which by the kindness of Dr. H. Woodward, F.R.S., I was allowed to make, failed to disclose any trace of the thyrohyals or the laryngeal skeleton.

In *Pipa* and *Xenopus* the third, fourth, and fifth digits of the hind limb are nearly equal in length, and in *Pipa* the third is if

anything longer than the fourth,—a feature unparalleled among living Anura (23. p. 178); and these facts acquire an exceptional significance when taken in conjunction with the observations of Wolterstorff, that in *Palæobatrachus* the third and fourth digits of the hind limb are either equal in length, or the third is but slightly shorter than the fourth (43. II. p. 16 [96], and I. p. 42). Further:—"Die Länge der Metacarpi, die stumpfe Beschaffenheit des Fusses haben *Palæobatrachus* und *Xenopus* mit *Pipa* gemeinsam" (43. II. p. 75).

Palæobatrachus is unique among Anura in having the diapophyses of the seventh, eighth, and ninth vertebræ confluent to form a disc, perforated by two foramina which mark the limits of the three diapophyses (43. p. 30). Among living Anura a multiple sacrum is only met with in *Pelobates* and *Pipa*, although it may occur exceptionally in the frog (Howes 21) and *Bombinator* (Götte 17; Camerano 5). In *Pelobates* and *Pipa* the expanded plate to which the ilium is attached is formed by the united diapophyses of the ninth and tenth vertebræ; and in the late embryo of *Pipa* (Stage VI., *antea*) there is present near the posterior edge of the plate a small triangular foramen which marks off the small transverse process of the tenth vertebra from the expanded diapophysis of the true sacral (ninth) vertebra. The outlines of the ninth and tenth vertebræ cannot be distinguished with certainty in the adult. In both *Pelobates* and *Pipa* the urostyle is immovably fused with the sacrum *. In *Xenopus* also the sacral diapophyses are greatly expanded, and the urostyle is confluent with the sacrum. The sacrum, however, is simple, and the lateral plates consist of the diapophyses of the ninth vertebra only. The tenth vertebra is not differentiated in *Palæobatrachus*, but is included, as it is in most Anura, in the urostyle. This latter is not confluent with the sacral vertebra, but articulates (43. p. 29) on to a pair of condyles situated on the posterior surface of its centrum.

There are eight free presacral vertebræ in *Xenopus*, but in *Pipa* only seven, the first two vertebræ not being differentiated from one another. In *Palæobatrachus* also the first two vertebræ are confluent, and, since the seventh and eighth enter into the formation of the sacrum, there are but five free vertebræ. The

* Cope's statement (6. p. 96 and 7. p. 252) that in *Pipa* the urostyle is simple and attached to a single condyle is, if not misleading, liable to misinterpretation.

vertebral column of *Pelodytes* does not differ materially from the normal. The first two vertebræ are not confluent as Cope states (6. p. 108).

In both *Xenopus* and *Pipa* the diapophyses of the third and fourth vertebræ are very long, and those of the fourth are terminated by a large backwardly-directed plate of cartilage. It has always been urged as an argument against associating the Aglossa with the Discoglossidæ, that the latter have free ribs on the second, third, and fourth vertebræ, while the former have no ribs. But in ripe embryos of *Pipa* (Stage VI., *antea*) the second and third diapophyses are segmented, and the peripheral portions correspond exactly with the second and third ribs of *Discoglossus*. The first diapophysis is short and unsegmented. The hinder of the two ribs is terminated by a backwardly-directed plate of cartilage. Both the ribs and the transverse processes proper are ossified, and the former are freely movable upon the latter. The remaining vertebræ have no autogenous ribs. In *Xenopus* larvæ (Stage II., *antea*) there are long, ossified, movable ribs attached to the third and fourth vertebræ, and a small pair to the second. The transverse processes are practically absent, so that the ribs arise directly from the neural arch. In larvæ of *Pelobates* and *Pelodytes* I have been unable to find ribs differentiated on the second, third, and fourth vertebræ, although I have examined four different stages of the former and three of the latter.

As already noted by von Ihering (Morph. Jahrb. vi. 1880, pp. 297–314) and Grönberg (18. p. 641), no trace of separation of the first vertebra into two parts can be detected in embryos of *Pipa*. But the fact of the first spinal nerve passing out *through* the neural arch, and the presence of but six other presacral vertebræ, point to the conclusion that two vertebræ are here represented. The occurrence in the embryo of diapophyses in connexion with this vertebra is a serious bar to the acceptance of the view propounded by von Ihering (*l. c.*) that in *Pipa* the second vertebra has been excalated, for in no anurous amphibian are diapophyses known to occur on the first vertebra.

In *Palæobatrachus* the vertebræ are sometimes procœlous and sometimes opisthocœlous. In *Pipa* and *Xenopus* they are opisthocœlous. But great importance cannot be attached to the characters of the articular surfaces of the centra, since it is a well-known fact (Dugès, 10. p. 107, Pl. 4. fig. 33; Cope, 7. p. 253;

Boulenger, 3. p. 482, and others) that in *Pelobates* and some other genera the intervertebral sphere may remain free in the adult, or may attach itself indifferently to the vertebra in front or that behind, causing them to become procœlous and opisthocœlous respectively. The extent of ossification of the frontoparietals is a character upon which Cope lays considerable stress in his classification. In *Pipa* and *Xenopus* the degree of ossification of the roof of the skull rather negatives their affinity with the Discoglossidæ, to which Cope (7. p. 248) considers them most nearly allied. The frontoparietal is strongly ossified in *Palæobatrachus*. In both *Pipa* and *Xenopus* the epicoracoid cartilages of the shoulder-girdle are in contact in the middle line, without overlapping or fusing, so that in this respect the Aglossa occupy a position intermediate between the Arcifera and the Firmisternia. There is no ossified xiphisternum, nor omosternum, and Cope regards the girdle, although a rigid one, as a modified variety of the arciferous type. Since the firmistern Anura are arciferous in early life, and since the girdle of *Pipa* and *Xenopus* cannot be conceived as originating by any modification of the raniform type, the probability of any affinity between the Aglossa and the firmistern Phaneroglossa is emphatically negatived.

In the limb skeleton the distal carpalia 3 and 4 are perfectly distinct in both *Xenopus* and *Pipa* (23. p. 161). This is a primitive character which brings the Aglossa near to *Pelobates* and the Discoglossidæ. But, on the other hand, the reduction of the skeleton of the pollex in *Xenopus* and *Pipa*, and the fusion of the second and third tarsalia of the distal row, are features indicating a degree of specialization not paralleled in the Discoglossidæ, *Pelobates* or *Pelodytes*. In the fusion of the ulnare with the postaxial centrale, *Pipa* differs not only from *Xenopus* but from all other Anura (23. p. 161). *Xenopus* possesses maxillary teeth, while *Pipa* is edentulous; but assuming that Cope is justified in discrediting the systematic value of the tooth-characters in Anura (7. p. 247), another great barrier between *Pipa* and *Xenopus* is broken down.

The extraordinary brood-pouches on the back of the female *Pipa* are not represented in *Xenopus*; but they cannot be regarded as of taxonomic importance, since brood-chambers of one kind or another are developed independently in widely-removed genera of Anura. The abnormality, amounting almost

to suppression, of the larval development in *Pipa* is of course directly related to the protected position which the embryos occupy on the back of the mother. The paired spiracular aperture of *Xenopus* larvæ is a primitive character, and the absence of a suctorial mouth with horny teeth shows less specialization than in more familiar tadpoles. The absence in *Pipa* and *Xenopus* of a persistent pre-renal part of the embryonic post-cardinal vein, which persists so frequently in the Discoglossidæ (22), is a sign of extensive departure from the primitive type. The epipubic cartilage of Urodela is represented in *Xenopus* by the racket-shaped cartilage in the postero-ventral body-wall; but it is not, so far as I am aware, found in any other Anura. It is not present in *Pipa*. In the retention also, by the adult, of the organs of the lateral line, and in the possession of claws on the first three digits of the hind foot, *Xenopus* is unique among Anura *.

In the characters of the shoulder-girdle, the genera *Pipa* and *Xenopus* would appear to be more closely allied to one another than to any of the Phaneroglossa †; and the characters of the muscular system recounted by Beddard, taken in conjunction with the anatomy of the hyobranchial apparatus set forth in the body of the present paper, and the features of the carpus and tarsus, tend in the main to show that, however much at variance they may be in many details of anatomical structure, the two genera, *Pipa* and *Xenopus*, have a true genetic relationship, and are not to be looked upon as the culminating members of parallel series. The suggestion of convergence put forward by Cope cannot yet be considered as finally disposed of, but the most recent evidence that has been brought to bear upon the question points towards a common ancestry of the two tongueless toads.

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* Since writing the above, Mr. G. A. Boulenger, F.R.S., has been good enough to demonstrate to me the presence of a persistent lateral line in *Leptobrachium monticola*, *Rana hexadactyla*, and various species of *Pseudis*, and has furnished me with a reference to his published allusion to the fact:—Ann. Mus. Genova (2), xiii. 1893, p. 344.

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EXPLANATION OF THE PLATES.

PLATE 8.

Fig. 1. *Xenopus lævis*, female. Hyobranchial and laryngeal skeleton, ventral view. (×3.)

2. *Xenopus lævis*, female. Right half of laryngeal skeleton, seen from within. (×3.)
3. *Xenopus lævis*, female. Laryngeal skeleton, dorsal view. (×3.)
4. *Xenopus lævis*, male. Laryngeal skeleton, ventral view. (×2½.)
5. *Xenopus lævis*, male. Laryngeal skeleton, in median section. (×2½.)
6. *Xenopus lævis*, male. Laryngeal skeleton, dorsal view. (×2½.)

In figures 2 and 5 the cut surfaces are marked by diagonal shading.

PLATE 9.

Fig. 1. *Pipa americana*, female. Hyobranchial and laryngeal skeleton, ventral view. (×3.)

2. *Pipa americana*, female. Laryngeal skeleton, dorsal view. (×3.)
3. *Pipa americana*, female. Laryngeal skeleton, median vertical section. (×3.)
4. *Pipa americana*, male. Internal or ventral view of the roof of the laryngeal skeleton, cut as indicated by the dotted line in fig. 6. (×1½.)
5. *Pipa americana*, male. Dorsal view of laryngeal skeleton after removal of the roof. (×1½.)
6. *Pipa americana*, male. Laryngeal skeleton, seen from the left side. The dotted line indicates the plane of section of figs. 4 and 5. (×1½.)
7. *Rana esculenta*, female. Right half of the laryngeal skeleton in median section. (×4.)

In figs. 3, 4, 5, and 7 the cut surfaces are marked by diagonal shading.

Reference letters to PLATES 8 *and* 9.

a. Ala, or great wing of the hyobranchial skeleton.
ap. Antero-lateral process of the basal plate.
ar. Arytenoid cartilage.
ar'. Posteriorly-directed process of the arytenoid cartilage.
bl. Blinker-shaped process of the cricoid cartilage. ("Scheuklappenartiger Fortsatz" of Henle.)
br. Bronchial cartilage.
c. Dorsal or roofing portion of the cricoid cartilage.
c'. Antero-ventral portion of the cricoid cartilage.
c''. Postero-ventral portion of the cricoid cartilage.
ch. Ceratohyal or anterior cornu.
ch'. Median rod of cartilage formed by the union of the anterior cornua.
cr. Crest arising from the floor of the larynx.
d. Process of the arytenoid to which the dilator muscle is attached.
ep. Posterior epiphysis of the thyrohyal.
f. Membranous area in the side-wall of the larynx.
f'. Membranous area in the floor of the larynx.

g.s. Area of insertion of the m. geniohyoideus externus.
gl. Position of the glottis.
h. Hyoglossal foramen.
i. Isthmus between the anterior and posterior portions of the basal plate.
i'. Ligament in the male *Pipa* equivalent to the cartilaginous isthmus of the female.
l. Ligament in the male *Xenopus* equivalent to the cartilage, *z.* fig. 1, of the female.
l'. Ligament binding the cricoid cartilage to the posterior epiphysis of the thyrohyal.
pc. Procricoid.
r. Ring of cartilage surrounding the aperture of the lung.
t. Thyrohyal.
v. Surface of articulation between the arytenoid rod and the roof of the larynx.
vc. Rudimentary vocal cord.
x. Posterior limit of the basal plate of the hyobranchial skeleton.
y. Anterior border of the basal plate.
z. Bar of cartilage connecting the ala with the basal plate.

PLATE 10.

Fig. 1. *Xenopus lævis*, female. Muscles of the ventral surface of the larynx. (×2⅔.)
2. *Xenopus lævis*, female. Muscles of the dorsal surface of the larynx. (×2⅔.)
3. *Xenopus lævis*, male. Muscles of the ventral surface of the larynx. (×2¼.)
4. *Xenopus lævis*, male. Muscles of the dorsal surface of the larynx. (×2¼.)
5. *Pipa americana*, female. Muscles of the dorsal surface of the larynx. (×3⅓.) At the top of the figure the three divisions of the hyoglossus are seen issuing through the hyoglossal foramen.
6. *Pipa americana*, female. Muscles of the ventral surface of the larynx. (×3⅓.)

Reference letters to PLATE 10.

a. Area of insertion of an ill-defined muscular tissue.
b. Bronchus.
c. M. compressor glottidis.
d. M. dilator laryngis.
d'. Accessory slip of the dilator muscle.
d.a. M. dilator laryngis anterior.
g. Glottis.
g.i. M. geniohyoideus internus.
h.e. M. hyoglossus externus.
h.i. M. hyoglossus internus.
o.i. Laryngeal tract of the m. obliquus internus.
p. M. petrohyoideus.

PLATE 11.

Fig. 1. *Xenopus lævis*, larva, stage 1. Hyobranchial skeleton, with mandible and larynx. (×3½.) Dorsal view.

2. *Xenopus lævis*, larva, stage 2. Hyobranchial skeleton, with mandible and larynx. (×4.)

3. *Xenopus lævis*, larva, stage 3. Hyobranchial skeleton, with mandible and larynx. (×6½.)

4. *Pipa americana*, embryo, stage 1. Hyobranchial skeleton, with mandible and larynx. (×8.) Dorsal view.

5. *Pipa americana*, embryo, stage 2. Hyobranchial skeleton, with mandible and larynx. (×7.)

6. *Pipa americana*, embryo, stage 3. Hyobranchial skeleton, with mandible. (×7.)

7. *Pipa americana*, embryo, stage 4. Hyobranchial skeleton, with mandible. (×6.)

8. *Pipa americana*, embryo, stage 5. Hyobranchial skeleton, with mandible. (×6.)

9. *Pipa americana*, embryo, stage 6. Hyobranchial skeleton, with mandible. (×6.) The position of the larynx is indicated by the dotted line.

10. *Xenopus lævis*, larva, stage 3. Laryngeal skeleton, dorsal view. (×12.)

11. *Pipa americana*, embryo, stage 6. Laryngeal skeleton, dorsal view. (×8.)

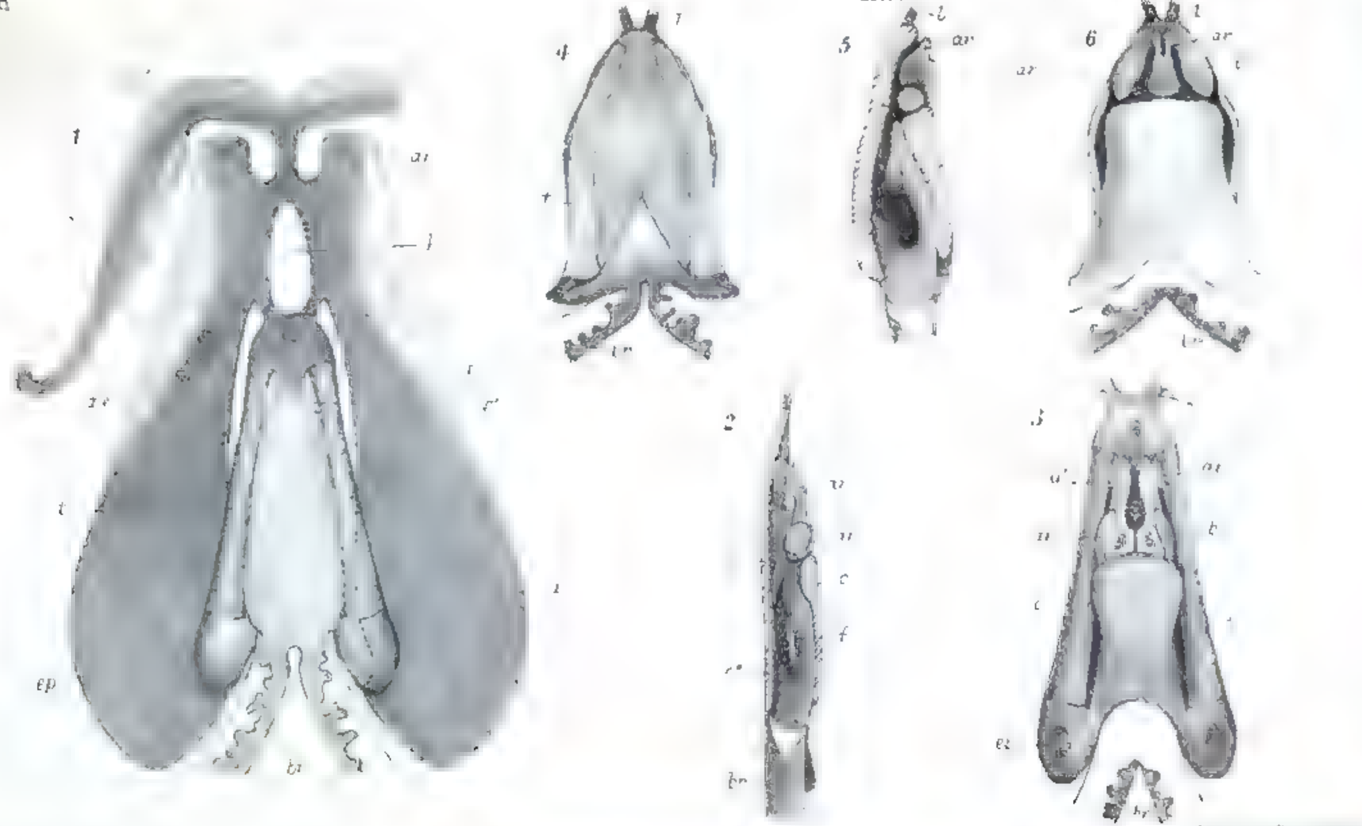
12. Same, ventral view.

13. *Bombinator pachypus*, adult female. Laryngeal skeleton, dorsal view. (×4½.)

Reference letters to PLATE 11.

a. Ala, or greater wing of the hyobranchial skeleton.
ar. Arytenoid cartilage.
b. Bronchus.
bh. Basihyal.
br. Bronchial cartilage.
cb.1. Ceratobranchial element of the first branchial arch.
ch. Ceratohyal.
ch'. Median rod of cartilage in front of the hyoglossal foramen.
cl.3. Third branchial cleft.
eb. Epibranchial or commissural cartilage.
g. Glottis.
g.e. Area of attachment of the m. geniohyoideus externus.
h. Hyoglossal foramen.
hb. Hypobranchial plate.
k. Overhanging cartilage on the antero-external edge of the branchial basket.
l'. Ligament connecting the cricoid cartilage and the posterior epiphysis of the thyrohyal.
m. Meckelian cartilage or mandible.
p. Accessory lobe of the lung arising from the dorsal surface of the bronchus.
t. Thyrohyal or posterior cornu.
t'. Thyroid foramen.
† Region of separation of the first ceratobranchial from the hypobranchial plate.

Ridewood



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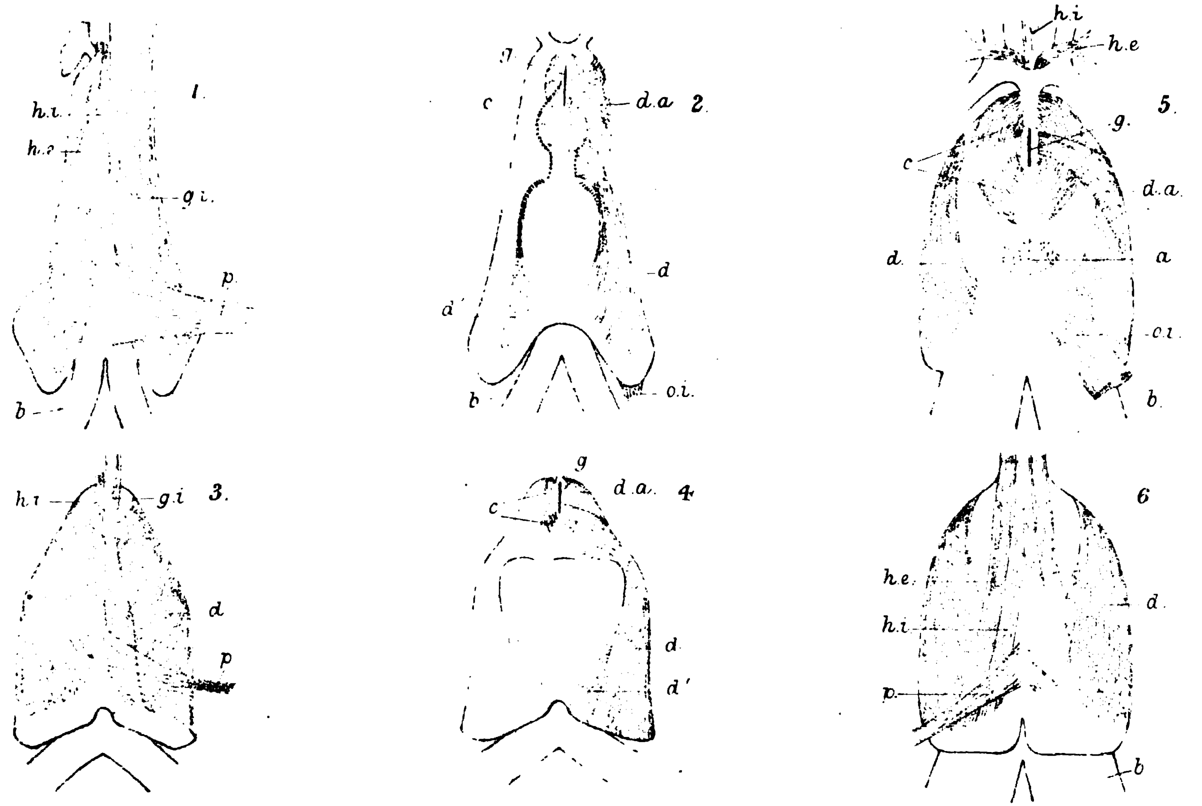
Mintern Bros imp

XENOPUS LÆVIS

W G R del. J Green lith

Mintern Bros imp

PIPA AMERICANA.



W. G. R. del. J. Green lith.

XENOPUS & PIPA.

Mintern Bros. imp.

W G R del. J Green lith.

XENOPUS & PIPA

adaptation can be pointed to in which we have *time data*, in which we can fix the maximum possible age of the variety; but very probably the dark Lepidoptera of the great Factory districts of England present such a case, and owe their existence to the smoky surroundings.

For an excellent summary of records of this kind in Insects, see Carpenter (4).

4

The study of such cases is a most fascinating one, as, owing to the limited number of factors at work, we may be able to trace, step by step, the causes and their modifying effects upon the species, and so to clear up many points as to the details of the process of elimination known as Natural Selection.

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EXPLANATION OF PLATE 30.

Varieties of *Mus musculus*.

The dark individual on the right-hand side is No. 4 in table (p. 466), the individual on the left is No. 27; that in the centre No. 30.

On the Larval Hyobranchial Skeleton of the Anurous Batrachians, with Special Reference to the Axial Parts. By W. G. Ridewood, D.Sc., F.L.S., F.Z.S., Lecturer on Biology at St. Mary's Hospital Medical School, London.

[Read 20th January, 1898.]

(Plate 31.)

Introduction.

The observations recorded in the following pages were made with the especial object of ascertaining whether the peculiarities of the larval hyobranchial skeleton of *Alytes* are common to all the genera of the family Discoglossidæ, and whether they occur in any genera not belonging to this family. The peculiarities in question consist in the presence of an anterior copula, and the complete separation of the hypobranchial plates by the posterior copula, which thus extends back to the laryngeal sinus, as already fully described in a communication recently presented to the Zoological Society, and appearing shortly in the 'Proceedings.'

Tadpoles of twenty-one species were examined, belonging to nineteen genera; and for all of the specimens I am indebted to Mr. G. A. Boulenger, F.R.S., whom I have always found most ready and anxious to encourage morphological enquiries of this kind, and to whom my thanks are hereby gratefully tendered. Considering how few of the species of Anura are known in their larval stages, the following list will be admitted to be very complete and representative.

The three numbers of the formula appended to each name stand respectively for the distance in millimetres from the snout to the root of the tail, the length of the tail, and the length of the hind limb. No measurement is given of the fore limb, because, in order to make the comparison between the different species as perfect as possible, the tadpoles were all selected at that stage in which the larval hyobranchial skeleton is most complete and most characteristic. This stage is recognized externally by the small size of the hind limbs, and by the fact that the fore limbs are not yet extruded through the atrial wall.

Ranidæ.			
Rana esculenta.	18.	24.	6.
Rana temporaria.	12.	22.	4.
Rana Whiteheadi.	10.	15.	2.
Oxyglossus lævis.	11.	29.	8.
Rhacophorus leucomystax.	16.	26.	10.
Phyllobates trinitatis.	5.	8.	0.
Engystomatidæ.			
Microhyla ornata.	6.	9.	2.
Cystignathidæ.			
Pseudis paradoxa.	41.	82.	28.
Telmatobius marmoratus.	35.	45.	7.
Chiroleptes platycephalus.	25.	34.	5.
Calyptocephalus Gayi.	41.	54.	9.
Bufonidæ.			
Bufo vulgaris.	12.	17.	3.
Hylidæ.			
Hyla arborea.	12.	22.	8.
Pelobatidæ.			
Pelodytes punctatus.	13.	16.	1.
Pelobates fuscus.	35.	60.	16.
Leptobrachium Hasselti.	24.	27.	9.
Discoglossidæ.			
Discoglossus pictus.	8.	11.	1.
Alytes obstetricans.	20.	35.	4.
Bombinator igneus.	16.	20.	6.
Dactylethridæ.			
Xenopus lævis.	25.	35.	6.
Pipidæ.			
Pipa americana.	10.	12.	4.

General Part.

The results of the investigation may be summarised in the following words:—The two fundamental peculiarities of the larval hyobranchial skeleton of *Alytes* above specified are found in the tadpoles of *Bombinator* and *Discoglossus*, but not in any of the other genera examined. This discovery is a lasting tribute to the perspicacity and intuition of the late Prof. Cope, who first brought together in taxonomic relationship the genera *Alytes*, *Discoglossus*, and *Bombinator*, which had previously been relegated

to three distinct families. Without entering into a discussion of the question whether the larval stages of Anura represent a true recapitulation of ancestral evolution, the similarity in the structure of the larval hyobranchial skeleton in these genera can, I think, be safely taken to indicate close genetic relationship.

The position of the anterior copula of the Discoglossidæ is in almost all the other forms examined occupied by loose connective tissue, the middle or hinder part of which is firmer and has the form of a transverse ligamentous band (fig. 2, *l*) connecting the ceratohyals. Gaupp, in his description of *Rana* tadpoles (4. p. 404), alludes to this band as being partially cartilaginous. Although I have failed to recognize anything approaching the structure of cartilage in the ligament, I fully concur with this author in regarding it as the morphological equivalent of the anterior copula of *Alytes*. I have not succeeded in finding the band in either *Pelodytes*, *Xenopus*, or *Pipa*.

Considerable diversity of form is observable in the shape of the second or posterior copula, and the proportion which it bears to the surrounding parts. It is usually longer than broad, but is broader than long in *Chiroleptes* (fig. 7, *cp.*) and *Telmatobius*. It is large in *Pelobates* (fig. 8), *Leptobrachium* (fig. 4), and the Discoglossidæ (fig. 1), but small in *Chiroleptes* (fig. 7) and *Phyllobates*.

Except in the Discoglossidæ, where the posterior copula extends back to the laryngeal sinus, the spaces at the right and left sides of the copula vary directly in size with the copula itself, being largest in *Pelobates* (fig. 8, *s*) and practically absent in *Phyllobates*. The hypobranchial plates are very variable in shape, the variability depending chiefly on the obliquity of their anterior edges and the length of their internal or mesial margins. These relations are themselves dependent on the proportionate size of the posterior copula. Thus, in *Chiroleptes* (fig. 7), the antero-lateral edges of the hypobranchial cartilages are very oblique and the median symphysis long, the copula being small and the lateral spaces small. The opposite extreme is exemplified by *Pelobates* (fig. 8), in which the anterior margin of the hypobranchial plate is strictly transverse and the symphysis short, these features being correlated with the large size of the copula and of its lateral spaces. *Hyla*, *Bufo*, and *Rana* (fig. 2) occupy intermediate positions between these extremes.

In early tadpoles, which alone are now under consideration, the posterior margin of the hypobranchial cartilage is but slightly indented by the laryngeal sinus, for the sides of this are bounded mainly by the spicula of the fourth branchial bar. This is absolutely the case in *Leptobrachium* (fig. 4, *ls.*), but the generalization does not hold good for the Discoglossidæ, and is only partially applicable to such genera as *Pseudis* (fig. 5) and *Rhacophorus*. In *Oxyglossus*, where there are no spicula, the laryngeal sinus is merely a notch at the back of the hypobranchial plate (fig. 6, *ls.*). The distinctness of the fourth spicula from the hypobranchial plates is most clear in *Leptobrachium* (fig. 4, *sp.*[4]), in which these cartilages are very large; they are but feebly differentiated in *Pseudis* (fig. 5). It is of some interest to note that the first ceratobranchial is fused with the cartilage of the hypobranchial plate in all the forms examined except *Alytes*, *Bombinator* * (fig. 1, *cb.*[1]), and *Discoglossus* (in which genera the union is effected by connective tissue), because in *Pelodytes* the basal portion of the bar persists as the processus posterolateralis of the adult hyoid (12. p. 590), whereas in *Alytes* the whole of the ceratobranchial skeleton is ultimately resorbed.

Microhyla, *Xenopus*, and *Pipa* are too exceptional to come within the scope of the foregoing generalizations, and these genera are, therefore, treated of only in the succeeding "Special Part."

The results of the present investigation cannot be said to have solved the problem of the morphological value of the hyobranchial copulæ of the Anuran larva. The most natural inferences to be drawn from the arrangement of the parts of the hyobranchial skeleton of the Discoglossidæ are that the anterior copula is the equivalent of the basihyal of the fish, and that the posterior copula is a basibranchial. But in such forms as *Rana* and *Pelobates* the single copula present is situated quite anteriorly to the branchial part of the skeleton; and although this fact does not prevent it still being regarded as a basibranchial (seeing that in *Notidanus* the basibranchial is situated anteriorly to the hypobranchial elements of the arch),

* This relation in *Bombinator* has already been pointed out by Götte (5. p. 679).

yet the deduction is unsatisfactory and inconclusive. That the single copula of the Ranid type of skeleton is the exact, or partial, equivalent of the posterior copula of the Discoglossid type is, I think, beyond question, in view of its close proximity to the pars reuniens, which latter is certainly homologous in the two cases.

The single copula of the Ranid type has been called the "basihyal" by Dugès (3) and the "basihyoid" by Schulze (14)*, while Parker (8) chose to name it the "basibranchial." But then Parker's nomenclature was seriously influenced by his regarding the pars reuniens as an essential constituent of the hyobranchial skeleton and his calling it, in consequence, the "basihyal" †.

The second basibranchial which Parker has described in *Calyptocephalus* and *Cyclorhamphus* cannot be allowed to carry much weight in the discussion. It is probably to be explained as an exceptional duplication of the single copula, if not as an error of observation, or as an accidental tearing of the cartilage in the dissection of the specimen (see p. 482).

Special Part.

Ranidæ.

The structure of the hyobranchial skeleton of the early larva of *Rana* has recently been so ably investigated by Gaupp (4), that I abstain from a full description of the parts. A figure is here given (fig. 2), not in order to illustrate any new features, but for the convenience of the reader of the following notes on those genera which are not figured but are compared as regards the structure of their larval hyobranchial skeleton with the common frog. The thoroughness of Gaupp's paper renders an historical summary also unnecessary, the earlier figures by Cuvier (2), Saint-Ange (13), Rathke (9), Reichert (10), Parker (7 & 8), Stöhr (15), and Naue (6) being criticised and effectually disposed of in this work. The only point on which I venture to differ

* Schulze does not include the pars reuniens in his "basihyoid" as Gaupp leads one to infer (4. p. 412). He calls it "eine querfaserige Bandmasse" (14. p. 9), corresponding with the "basihyal" of Parker, and he figures it quite distinct from his cartilaginous "basihyoid" (14. Taf. 1. fig. 5).

† The exceptional chondrification of the pars reuniens in *Microhyla* (p. 481) does not, in my opinion, entitle it to rank as a morphological unit in the larval hyobranchial skeleton, any more than a sesamoid chondrification in a tendon is to be considered as a morphological constituent of the limb-skeleton.

from Dr. Gaupp is in his interpretation of "connective tissue," a matter to which I have already referred in an earlier communication (11. p. 97). Dr. Gaupp's figures of the early hyobranchial skeleton show all the constituent cartilages perfectly continuous, whereas in specimens dissected under spirit there can be seen a distinct differentiation of tissue at the line of junction of certain parts, along the hypobránchial symphysis for instance. This tissue is yellowish and opaque, and frequently stands out in strong contrast with the hyaline cartilages on either side of it, and this it is which has been called "fibrous tissue," "connective tissue," "Bindegewebe," etc. by various authors. When, however, sections are cut and, after staining and clarifying, are examined under the microscope, all this differentiation disappears. The cells of the "connective tissue" are slightly smaller and are more closely packed than those of the hyaline cartilage, but the two tissues graduate so insensibly into one another that histological differentiation is denied by those who adopt this method of investigation only. The difference of opinion between Gaupp (4. p. 415) and Naue (6. p. 139) as to the mode of connection between the last three branchial bars and the hypobranchial plate, is solely dependent on this question. There is certainly a difference between the mode of attachment of the first and the following arches, for, when seen under a lens, the first ceratobranchial is so continuous with the hypobranchial plate that no line of junction can be discerned, but in the case of the other three there is a faint yellow line which marks the limit of the hypobranchial cartilage. This line indicates the position of the "connective tissue," and by declining to admit the existence of this tissue Gaupp is forced to deny the difference in the distinctness of the limits of the proximal ends of the first and the remaining three branchial arches, a difference which in such a Ranid as *Oxyglossus* is so marked as to be visible to the naked eye.

No difference whatever is to be seen between the hyobranchial skeletons of early larvæ of *Rana esculenta* and *Rana temporaria* (fig. 2). The tadpoles are so much alike that this perhaps is not surprising. But some palpable difference was to be expected in the third species examined, for in *Rana Whiteheadi*, as in the genus *Micrixalus*, the tadpole is provided with a large suctorial disc, extending nearly the full width of the body, and occupying about half the distance between the mouth and cloaca. This

sucker, which in all probability represents the persistent and greatly enlarged ventral sucker which in our common frog is characteristic of the very early larvæ breathing by external gills, enables the tadpoles to adhere to rocks and stones in the mountain torrents in which they live. It gives a most singular appearance to the tadpole, but appears not to affect the internal organs. The hyobranchial skeleton, at all events, differs from that of *R. temporaria* only in that the internal or mesial parts of the ceratohyals are more expanded, and that the hypobranchial symphysis is shorter.

Rhacophorus differs from *Rana* only in the shallowness of the hyoglossal sinus, and in the fact that the hyobranchial plates are longer than broad, the reverse obtaining in the frog. The early tadpole of *Oxyglossus* possesses a hyobranchial skeleton which is remarkable for the relatively great size of the hyoid arch and the small development of the branchial system. The width of the branchial part of the skeleton is much less than that across the hyoid even at this early stage (see fig. 6). Filling the hyoglossal sinus and projecting some little distance in front of it, is a dense fibrous mass in which the normal transverse ligament is not clearly differentiated. The branchial bars are short, thin, and straight, and have no spicula. The first ceratobranchial is confluent with the hypobranchial cartilage, while the other three are attached by means of a well-marked fibrous tissue. Since there are no fourth spicula, the laryngeal sinus is very shallow; but it probably deepens later by absorption of the hypobranchial cartilage. The spaces at the side of the copula are well defined and triangular in shape. The pars reuniens is but feebly developed, and the ceratohyals touch one another in the median line.

The specimen of *Phyllobates* examined was one taken from the back of the father, to whose skin the tadpoles adhere in time of danger. The hyobranchial skeleton differs from that of *Rana* chiefly in the greater relative size of the hypobranchial plates and the corresponding smallness of the copula. The symphysial line disappears in the posterior third, so that the two hypobranchial plates are fused here. The first ceratobranchial is confluent with the hypobranchial plate, while the other three adhere by fibrous tissue, as in *Rana*, *Oxyglossus*, *Rhacophorus*, and probably in many other genera. Spicula are present, but they are proportionately shorter and more stunted than in *Rana*.

In spite of the extreme minuteness of the whole hyobranchial skeleton, such features as the ligamentous band in the hyoglossal sinus and the space at the side of the copula can be easily made out by ordinary dissection.

ENGYSTOMATIDÆ.

The tadpoles examined were collected in Siam and presented to the Natural History Museum, London, by Mr. Stanley Flower, and were reported by him to be the offspring of *Microhyla ornata*. They bear a remarkable resemblance to the larvæ of *Xenopus* of the Cape, in shape, general transparency, and the silvery appearance of the abdomen.

The hyobranchial skeleton is most singular (fig. 3). The hypobranchial plates are fused across the median line, and have a thickened anterior margin which is fused with the hind end of the copula. The place where the pars reuniens normally occurs is occupied by a transverse bar of cartilage, fused at its extremities with the ceratohyals. The postero-internal parts of the ceratohyals are free, and overlap the anterior edge of the hypobranchial plate. The hyoglossal sinus is shallow, and the transverse ligamentous band is very distinct. The ceratobranchial skeleton has the form of a pair of great pouches perforated at the bottom by three slits, and in this respect, also, the tadpoles under consideration resemble *Xenopus*. The laryngeal sinus is narrow and deep, but owing to the fourth ceratobranchials being in contact with one another behind it, as in *Xenopus*, the larynx itself is situated very far back.

It would be interesting to ascertain what are the conditions of life which have evidently been instrumental in bringing about these external and these skeletal resemblances between two such remotely allied genera as *Microhyla* and *Xenopus*. That the two results have been arrived at independently is, I think, beyond question, for although the resemblances are so striking at first glance, the similarity does not extend into the smaller structural details.

CYSTIGNATHIDÆ.

Of the four genera examined, two (*Chiroleptes* and *Telmatobius*) resemble one another so exactly in the structure of their larval hyobranchial skeleton that one of them may be dismissed at once. *Pseudis* differs from these in several respects, notably

in the size of the space at the side of the copula, which is large in *Pseudis* (fig. 5, *s*) but extremely small in *Chiroleptes* (fig. 7). The copula itself is longer in *Pseudis*, and the pars reuniens is broader. Owing probably to the shortness of the copula in *Chiroleptes*, the hypobranchial symphysis is much longer in this genus than in *Pseudis*. The fourth pair of spicula are normal in the former, but are greatly expanded and fused with the third pair in *Pseudis*; a feature already alluded to and figured by Parker (8. p. 73, pl. 10. fig. 6, and pl. 11. fig. 4, *c. br.* 3–4), although in his figures the shape of the parts is not quite correct. In the earlier figure by Cuvier (2. pl. xxiv. fig. 22) this point is not evident.

Parker has also figured (8. pl. 17. fig. 4) the hyobranchial skeleton of a tadpole which, with some reserve, he identifies as *Cystignathus*. The figure, however, calls for no special comment. Two other genera of the Cystignathidæ were also examined by this author, and in both (*Calyptocephalus Gayi*, 8. pl. 22. fig. 5, and *Cyclorhamphus culeus*, pl. 22. fig. 9) a double basibranchial described and figured. Seeing how important from a morphological point of view the occurrence of two successive basibranchials would be, it is somewhat surprising that the author did not lay more stress upon the observation. Now the *Cyclorhamphus culeus* examined by Parker is a *Telmatobius* (probably *Telmatobius Jelskii*, see 1. p. 191); and since the double copula does not occur in the *T. marmoratus* examined by me, a shadow of suspicion naturally arises. To submit the matter to the final test, I applied to Prof. Lataste for permission to examine one of the tadpoles of *Calyptocephalus Gayi* from Chili, belonging to his private collection, and he most graciously responded. There is in Prof. Lataste's specimen no trace of a second copula behind the pars reuniens, but the whole hyobranchial skeleton is perfectly normal, and occupies a position midway between those of *Chiroleptes* and *Pseudis* in the proportions of the pars reuniens, copula, lateral spaces, and fourth spicula. It is evident, therefore, that no great weight can be attached to this observation of Parker's.

Bufonidæ.

The hyobranchial skeleton of *Bufo* does not differ greatly from that of *Rana*. The anterior edge of the hypobranchial cartilage is more oblique, and a different shape is in consequence given to

the triangular space at the side of the copula. The width of the copula is only one half that of the pars reuniens, whereas in *Rana* the two are nearly equal in breadth. The larynx is exceptionally far back, being nearly in a line with the posterior extremity of the fourth ceratobranchial. In no early Anuran tadpole does the larynx actually lie in the laryngeal sinus, for the latter name is anticipatory, and refers to a space which, in the adult, lodges the larynx; but in *Bufo* the larynx is farther removed from the sinus than is usual in larvæ of this stage.

HYLIDÆ.

In the proportions of the pars reuniens, the copula, and the spaces at the sides of the latter, the larval hyobranchial skeleton of *Hyla* approaches more closely to that of *Rana* than does that of *Bufo*. The first three pairs of spicula are a little longer than those of the frog, but the difference is slight. The line of demarcation between the hypobranchial cartilage and the fourth spiculum cannot be made out, the two cartilages being more continuous than in *Rana*.

The larval skeleton of *Nototrema* was examined by Parker, but not figured. It is described as being quite normal (**8.** p. 188). The meagre figure of *Hyla* by Stohr (**15.** Taf. iii. fig. 11) shows only the hypobranchial cartilages and the basal ends of the ceratobranchials confluent with them.

PELOBATIDÆ.

The three genera examined exhibit considerable uniformity of structure. The space at the side of the copula is large and triangular, the symphysial line between the hypobranchial plates is shorter than the antero-posterior diameter of the copula, and the ceratohyals are large in proportion to the branchial skeleton. The larval hyobranchial skeleton of *Pelobates* has already been figured by Dugès (**3.** Taf. xiii. fig. 75) and Schulze (**14.** Taf. i. fig. 5), and that of *Pelodytes* by myself (**12.** fig. 1).

The fibrous band which so commonly stretches across the hyoglossal sinus is clearly distinguishable in *Pelobates* and *Leptobrachium*; but on examining my former preparations of *Pelodytes*, and several new ones as well, I am still unable to detect it in this genus. The copula is considerably longer than broad in *Pelobates* (fig. 3, *cp.*) and *Leptobrachium* (fig. 4), but it is somewhat more hexagonal in *Pelodytes*. The pars reuniens in *Pelo-*

dytes is correspondingly long in an antero-posterior direction, while the outline of this fibrous mass is nearly square in *Pelobates* and *Leptobrachium*.

The lateral parts of the ceratohyals are exceptionally massive in *Leptobrachium*, and this genus is also remarkable in having the incipient laryngeal sinus bounded laterally, not by the hypobranchial cartilage tipped with the spiculum of the fourth branchial arch, but by the spicula alone (fig. 4, *ls.*). These latter are so largely developed as to simulate early and autogenous thyrohyals. In fact their exceptional proportions in this early stage may actually affect the later development of the thyrohyals. I have been unable to procure older larvæ of *Leptobrachium* to determine this point.

Discoglossidæ.

As already mentioned in the earlier part of this paper, there is a remarkable similarity in the structure of the larval hyobranchial apparatus in the three genera *Alytes*, *Bombinator*, and *Discoglossus*. The characters which they have in common, and which do not occur in any other Anuran larva examined, are:—the presence of an anterior copula in front of the pars reuniens, and the complete separation of the two hypobranchial plates by the large posterior copula situated behind the pars reuniens. I have already stated, in a paper presented to the Zoological Society in November 1897, that the credit of the discovery of the anterior copula of *Alytes* belongs to Gaupp (4. pp. 411–412). The figure which Götte has given of the larval hyobranchial skeleton of *Bombinator* (5. Taf. xviii. fig. 332) shows very well the extremely small size of the cleft between the third and fourth ceratobranchials, but the axial parts of the skeleton are rather indistinct. Three areas, probably representing the anterior and posterior copulæ with the fibrous pars reuniens between, can be distinguished, but no special notice is taken of the relations or the morphology of the parts. The earlier figures of *Bombinator* by Reichert (10. Taf. i. figs. 20 and 23) are so imperfect as to call for no detailed criticism.

In all three genera the transverse diameter of the anterior copula is greater than the longitudinal, and the copula is separated from the pars reuniens by a small space—quite minute in *Discoglossus*. The space between the antero-lateral border of

the second copula and the ceratohyal is very narrow in all three. Since a figure of the larval hyobranchial skeleton of *Alytes* is now appearing in the 'Proceedings' of the Zoological Society, and since the differences between *Discoglossus* and *Bombinator* are so slight, a figure of the hyobranchial skeleton of this last genus satisfies the requirements of the present communication (fig. 1).

Dactylethridæ and Pipidæ.

These two families may be shortly disposed of by referring the reader to my earlier remarks on the development of the hyobranchial skeleton of *Xenopus* and *Pipa* (11. pp. 91–111). It is impossible to say whether *Pipa* comes nearer to the Discoglossid or to the Ranid type of larval hyobranchial skeleton, for no copula can be distinguished, the whole cartilage being uniform and continuous throughout (11. pl. xi. fig. 4). No spicula are present, and the hyoglossal and laryngeal sinuses are, even in this earliest stage investigated, already deep. A re-examination, however, of my youngest specimens of *Xenopus* shows that the outline of the copula (11. pl. xi. fig. 1, *bh*) is more sharply defined than the figure would suggest, and that a long, narrow, faintly-outlined pars reuniens connects the anterior parts of the ceratohyals together and involves the thin end of the copula. There is nothing resembling an anterior copula, and the hyoglossal sinus is merely a small V-shaped notch. The hypobranchial part of the skeleton is reduced in size, and is wedged in between the copula and the great ceratobranchial pouches. It tapers to a point behind, far removed from the larynx, which occupies a very posterior position. The obvious conclusion to be drawn from the absence of a copula in front of the pars reuniens and the union of hypobranchial cartilages behind the posterior copula, is that the hyobranchial skeleton does not conform to that of the Discoglossid larvæ.

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E. Drake

HYOID OF LARVAL ANURA

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EXPLANATION OF PLATE 31.

All the figures represent the hyobranchial skeleton of early tadpoles, the measurements of which are given on p. 475. Except in figs. 3 and 6 the ceratobranchials are shown only on one side of the figure, or are not shown at all. All figures exhibit the dorsal aspect; and the magnification is expressed by the usual symbols in the Plate.

Fig. 1. *Bombinator igneus.*
2. *Rana temporaria.*
3. *Microhyla ornata.*
4. *Leptobrachium Hasselti.*
5. *Pseudis paradoxa.*
6. *Oxyglossus lævis.*
7. *Chiroleptes platycephalus.*
8. *Pelobates fuscus.*

Reference Letters.

ca. Anterior copula (fig. 1).
cb.[1] First ceratobranchial.
ch. Ceratohyal.
cp. Posterior copula in fig. 1; the copula in figs. 2–8.
hbr. Hypobranchial plate.
l. Ligamentous band in the hyoglossal sinus.
ls. Laryngeal sinus.
pr. Pars reuniens.
s. Space at the side of the copula.
s.[1] Space between the anterior copula and the pars reuniens (fig. 1).
sp.[4] Spiculum of the fourth branchial arch.

The "Porus genitalis" in the *Myxinidæ*. By R. H. Burne, B.A., Anatomical Assistant in the Museum of the Royal College of Surgeons of England.*

[Read 20th January, 1898.]

(Plate 32.)

Since the days of Johannes Müller † no detailed investigation has been made into the coarse anatomy of the cloacal region of the Myxinoids; subsequent anatomists ‡ having for the most

* Communicated by Prof. G. B. Howes, Sec. Linn. Soc.

† Johannes Müller, "Untersuch. über die Eingeweide der Fische," Abhl. d. k. Akad. Wiss., Berlin, 1843, p. 113.

‡ Vogt & Pappenheim, "Organes de la génération des Vertébrés." Ann. Sci. Nat. sér. 4, xi. 1859, p. 345; W. Müller, "Urogenitalsystem des Amphioxus u. der Cyclostomen," Jena. Zeitschr. ix. 1875, p. 109.

part dealt with the related family of the Lampreys, or contented themselves with a summary of Müller's original description of *Myxine glutinosa*. An exception must be made, however, in favour of Ewart *, for, at the end of a paper on the genital pores and surrounding parts of the Lamprey, he devotes a few lines of original description to the same organs in *Myxine*. Yet, on the whole, our present information upon this subject is so scanty and, as will appear later, inaccurate, that I venture to put forward the following brief description and drawings of the anatomy of the cloacal region in *Myxine glutinosa* and *Bdellostoma cirrhatum*, in the hope that they may form an appendix to the excellent description given by Ewart of these parts in the Lamprey.

According to Ewart, " the intestine of the Lamprey is a straight tube which lies free in the abdominal cavity, except near its termination, where several fine bands—the remains of the mesentery—fix it to the under surface of the notochord." The body-cavity, after the intestine has reached the ventral body-wall on its way to the anus, is continued on either side in the form of a blunt cone, near the apex of which a small aperture leads into a pyriform chamber (the uro-genital sinus). The base of the uro-genital sinus is in open connection with the ureters, and the apex projects freely into an integumentary pit, into which it opens close behind the anus. Thus we have a pair of internal "pori genitales" opening on either side from the body-cavity into a uro-genital sinus, and a single median external pore opening from the latter into the cloaca. Such appear to be the essential features of Ewart's description; but before leaving the Lamprey there are two minor points upon which I would comment. Ewart makes a great feature of the blunt ending of the body-cavity and its backward extension (1 line) beyond the "genital pores," and infers therefrom an error of observation on the part of Müller, who speaks of the "genital pores" having the form of a pair of tubes, one on either side of the rectum, that open at their ends into the uro-genital sinus. An examination of the cloacal region in the River Lamprey suggested to me that the discrepancy between these two accounts might very possibly be due to the description of a different species in either case. Müller, we know, examined both the Sea and River Lamprey

* J. C. Ewart, "Note on the Abdominal Pores and Uro-genital Sinus in the Lamprey," Journ. Anat. and Phys. x., 1876, p. 493.

(*Petromyzon marinus* and *fluviatilis*); but, as his description applies to the river form alone, one cannot avoid the suspicion that, although he may have cursorily examined *P. marinus*, his real observations were confined to *P. fluviatilis*. Ewart does not in his paper mention the species of Lamprey used, but through the kindness of my friend Professor Howes, F.R.S., I have ascertained that it was *P. marinus*; a conclusion to which I had been led by a comparison of his description with a dissection of that species. In this way the conflicting statements appear to admit of explanation. Then, again, with reference to the opening of the ureters into the uro-genital sinus, it should perhaps be more emphatically mentioned that the passage of the one into the other is gradual and imperceptible; the ureters, in fact, meet in the mid-line, coalesce and dilate to form the sinus; there is no papilla or any other mark to show where the one ends and the other begins.

As concerns *Myxine glutinosa*, in which the "pori genitales" are described as essentially similar to those of the Lamprey, I find a very different state of affairs, of which the following is a description (fig. 1) based upon the dissection of six specimens, checked by the examination of a series of transverse sections through a seventh *.

When the creature is placed upon its back, the mouth of the cloaca has the appearance of a narrow longitudinal slit some 10 mm. long, bordered by somewhat protuberant lips. The slit leads into a small chamber (fig. 1, *cl.*) flattened from side to side, and having roughly the form of an isosceles triangle placed in such a position that one of its sides corresponds to the cloacal slit and its short base to the anterior wall of the cloacal chamber. In the walls of this chamber there are four openings: two, of large size, in the anterior wall placed vertically one above the other, the anus below and the genital pore above (fig. 1, *an. p.g.*); and a smaller pair belonging to the ureters, situated close side by side on a papilla halfway along the dorsal wall (fig. 1, *ur.o.*). The dorsal and lateral walls of the cloacal chamber are raised into several longitudinal ridges that can be separated into a lower series continuous with the rectal rugæ, and an upper originating from the margin of the pore. Between these two

* These specimens of *Myxine glutinosa* were obtained from the Bergen Museum for the Royal College of Surgeons, some preserved in spirit, some in formalin.

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series the lateral parts of the dorsal lip of the anus extend backwards some little distance, forming a short but prominent lateral ridge; and in the dorsal mid-line another prominent ridge is formed by the inpushing of the ureters on their way to open on the urinary papilla. Behind the papilla the ridge is continued on, though diminished in size, to the posterior limit of the cloaca.

The intestine in *Myxine* is suspended by a dorsal mesentery, continuous to within some 6 or 7 mm. of the posterior extremity of the body-cavity (Pl. 32. fig. 1, *mes.*); on its ventral aspect it is free, but at a point 10 mm. in front of the anus it meets the ventral body-wall, within which it becomes gradually embedded as it bends downward towards the anus: in consequence the posterior end of the body-cavity becomes rapidly constricted and confined more and more to the dorsal surface of the intestine, until at a point directly above the anus it is entirely dorsal in position, and opens by a single pore of 1·2 mm. breadth into the cloaca (fig. 1, *p.g.*). The peritoneal lining of the body-cavity becomes thicker and closer in texture as the pore is approached, till round the actual orifice of the pore it forms a stout band (fig. 1, *fb.bd.*) of white fibrous tissue extremely rich in small round or pointed cells. Just before the anal opening is reached a gland (fig. 1, *sl.gl.*) makes its appearance in its upper lip, and as we pass backward gradually extends upward on either side into the lateral walls of the genital pore, and finally forms a complete circle by meeting in the dorsal mid-line. The chief part of the gland is situated in the dorsal lip of the anus and lateral walls of the pore, and is formed of several lobes or divisions separated one from the other by strands of connective tissue, from which yet finer strands are given off that subdivide the lobes into smaller compartments or lobules. Each lobule contains one or more spider-cells, and now and again one of the peculiar "thread-cells" characteristic of the lateral slime-glands, though the number of these is comparatively limited. The lobes have the form of flattened cones lying side by side with their apices directed forward; the bases of the cones are open, and so placed that they form a semicircle of openings round the ventral and lateral parts of the posterior margin of the pore; the extension of the gland upon the dorsal wall of the pore has the form of open glandular grooves. The openings of the gland correspond to the grooves between the upper series of cloacal ridges mentioned previously,

while the ridges themselves are formed by a backward extension of the interlobular connective tissue. In other words, the grooves between the upper series of cloacal ridges have at their anterior ends the structure of the lateral slime-glands, and are prolonged as glandular conical pockets for some distance into the lateral and ventral walls of the pore. I have gone at some length into the structure of this gland, as I believe that hitherto the features peculiar to the lateral slime-glands have been found there, and nowhere else*.

The ureters (fig. 1, *ur.*) run one on either side of the dorsal mid-line, outside the peritoneum; towards the posterior end of the body-cavity they approach each other, then run backward close side by side upon the dorsal wall of the cloaca, and finally open into it by a pair of slit-like openings upon the urinary papilla (fig. 1, *ur.o.*).

In addition to *Myxine glutinosa* I have been able to make a dissection of *Bdellostoma cirrhatum*, and find that in this genus the "porus genitalis" differs in several points from that of *Myxine*. In the first place the pore (fig. 2, *p.g.*) is very large, extending for 6 mm. on either side of the middle line; it is also situated considerably farther forward than in *Myxine*, lying 14 mm. in front of the anus instead of directly above it. The forward position of the pore is accompanied by a corresponding forward extension of the cloacal chamber upon the dorsal surface of the rectum, and by the obliteration of the unpaired portion of the body-cavity that in *Myxine* lies between the posterior edge of the dorsal mesentery and the pore. Thus we are practically dealing with a pair of genital pores, each 6 mm. broad, lying close side by side upon the dorsal surface of the rectum and separated one from the other by the edge of the mesentery. At first sight, one is sorely tempted to regard this condition as intermediate between the paired lateral pores of the Lamprey and the single median pore of *Myxine*—a step in the formation of a dorsal pore by the coalescence of a pair of lateral pores; but this is probably not the case. For when we notice that the body-cavity of *Bdellostoma* does not extend backward beyond the position of the edge of the mesentery in *Myxine*, and that the end of the rectum covered in *Myxine* by peritoneum is in *Bdellostoma* clothed by a highly specialized extension of the cloacal epi-

* Bloomfield, "The Thread-cells and Epidermis of *Myxine*," Quart. Journ. Micr. Sci. xxii., 1882, p. 355.

thelium, while the rest of the cloaca with the anal and ureteric openings has much the same form and proportions as in *Myxine*, we must consider that this region in *Bdellostoma* is in a less simple and generalized condition than in *Myxine*, and that the division of the pore is most likely a secondary modification brought about by its apposition to the edge of the mesentery in consequence of the forward extension of the cloaca,—in fact an incident in the history of the pore after, and not before, its assumption of the single condition; so that although, to all intents and purposes, *Bdellostoma* has two genital pores, morphologically it, like *Myxine*, has but one. The peritoneal thickening that surrounds the pore is well-developed and seems, so far as the imperfect preservation o the material at my disposal shows, to be more fibrous and less cellular than in *Myxine*; it is thicker above and below than at the extreme lateral points, giving to the pore in its normal state the form of a long narrow slit with its dorsal and ventral surfaces closely apposed.

The portion of the cloaca between pore and anus (fig. 2, *cl.ex.*) is raised into a number of longitudinal laminæ arranged somewhat as follows:—In the dorsal mid-line there is a very conspicuous single lamina, followed on either side after a small smooth space by a group of about 12 laminæ of slightly smaller size, arranged close side by side, parallel one to the other; upon the ventral wall the laminæ have a similar arrangement, though none of them are quite so strongly marked. The space between the laminæ is filled with a quantity of sticky slime, which is seen under the microscope to correspond to the secretion of the lateral slime-glands. The failure of transverse sections to show any communication between this part of the cloaca and the lateral slime-glands, in addition to the presence of a slime-gland round the abdominal pore in *Myxine*, would lead one to expect that the laminæ are the seat of the secretion of the slime. Unfortunately the state of preservation prevents my saying anything very definite upon their histology; but the following points seem fairly clear and, so far as they go, support the notion that this region of the cloaca is a slime-gland. The laminæ are supported by a central sheet of connective tissue, from which are given off subsidiary branches that now and again anastomose with one another; the connective-tissue support is clothed by a deep epithelium, often broken up by finer anastomosing strands of connective tissue into round glandular-looking follicles: whether

some of these are in reality spider-cells I cannot definitely say, but thread-cells can be certainly seen here and there buried in the tissues.

From the foregoing descriptions, the great difference that exists between the Myxinoids and their nearest relatives—the Lampreys—with regard to their "pori genitales" has, I trust, been made sufficiently clear. The explanation of the difference is most likely bound up with the function performed by the pores, for in the Marsipobranchii their chief duty is important enough to account for any suitable modification of their structure, since they form the sole passage by which the generative products can reach the exterior. The "genital pores" in the Lamprey, in which the reproductive elements are small (the ova being about the size of a small shot), are, as we have seen, paired and of such size (·5 mm. in *P. fluviatilis* *) that, under pressure of the ripe ova in the body-cavity, they expand enough to allow of their passage †. On the other hand, the Myxinoids possess ova few in number but large in size (a fairly ripe ovum of *Myxine* being a spindle-shaped body 19 mm. in length by 7 mm. in diameter, and that of *Bdellostoma* 31 mm. in length and 9·5 mm. in diameter). For the passage of such an ovum, pores similar to those of the River Lamprey would be clearly too small and certain to suffer extensive rupture if the ovum succeeded in making its exit. But instead of such pores, we find in *Myxine* a single median pore of very considerable size, and in *Bdellostoma* an enormous pore divided into two, in both cases admirably suited for the passage of a large-sized egg. For not only is the aperture large, but, to guard against any possible danger of rupture, it is encircled by a stout band of connective tissue, uncalled for in the case of the Lamprey with smaller eggs. What the special use of the slime secreted round the edge of the pore in *Myxine*, and more copiously in the anterior cloacal prolongation of *Bdellostoma*, may be, it is not very easy to say. It may of course have a certain lubricating effect in oviposition; but to judge from the

* These remarks do not apply to the Sea Lamprey, in which the pores are larger than the size of the egg would appear to warrant. Ewart speaks of their diameter as nearly 2 lines in the species examined by him (*P. marinus*), and in a specimen in the Royal College of Surgeons Museum I find them fully that [illegible]

† Galliver (Proc. Zool. Soc. 1870, p. 848) found 51,220 ovarian eggs in *P. fluviatilis*, and gives $\frac{1}{50}$ in. as their diameter; in *P. Planeri* the diameter was about $\frac{1}{20}$ in.

direct relation that exists between the quantity of slime secreted and the size of the pore, it looks as if it might answer somewhat the same purpose as the wax secreted in our own external auditory meatus, by preventing the intrusion of foreign matter, animate or inanimate, into the body-cavity, a danger to which the possessor of two contiguous pores, each 6 mm. broad, would seem to be especially exposed.

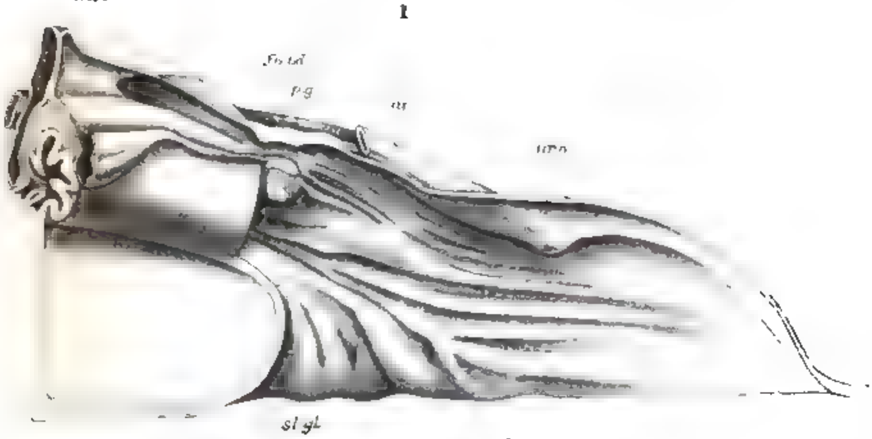
It will have been observed that the main difference between the Lampreys and Myxinoids lies in the absence in the latter of the direct communication between the "porus genitalis" and the uro-genital sinus that forms so characteristic a feature in the former. The apparent absence of the uro-genital sinus in the Myxinoids is, I am aware, generally explained by regarding the upper part of the cloacal chamber as its representative; but the following features seem to indicate that its absence is not apparent, but real. Although there seem to have been some contradictory statements made * in regard to the development of the cloaca in the Lamprey, yet the following account, taken from a recent detailed paper on the transformation of Ammocœte to Lamprey †, may probably be considered as fairly representing the truth:—The segmental ducts open originally into the posterior region of the gut, and then, during the passage of the Ammocœte into the Lamprey, their posterior ends fuse to form a common chamber into which, as it gradually separates from the gut and acquires an opening into an integumentary cloacal pit, the hitherto blind posterior prolongations of the body-cavity open, forming the "genital pores." So that in the adult we can sharply distinguish an uro-genital sinus, formed by the fusion of the segmental ducts, from an integumentary cloacal pit into which it opens. Now in the adult Myxinoid the ureters do not imperceptibly pass into the cloacal chamber, as they do into the uro-genital sinus of the Lamprey, but open upon a raised papilla; upon the margin of the ureteric opening, the epithelium changes its character—inside it is similar to that lining the rest of the ureter, outside it is epidermic. The whole cloacal chamber, both in *Myxine* and *Bdellostoma*, is lined by epidermis. For these reasons I am inclined to consider that the uro-genital sinus of the

* Ayers, "Untersuchungen über Pori abdominales," Morph. Jahrb. x. (1885) p. 346.

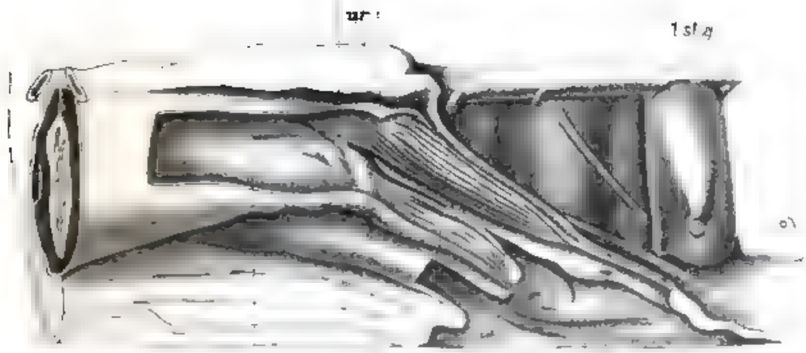
† Bujor, "Métamorphose de l'*Ammocœtes branchialis* en *Petromyzon Planeri*," Rev. Biol. Nord France, iii. (1891) p. 484.

5

1



2



R H B. del.
Parker & Percy lith.

Geo West & Sons imp.

PORUS GENITALIS IN THE MYXINIDÆ

Lampreys is absent in the Myxinoids, and that in the latter the anus, "porus genitalis," and ureters open into an integumentary cloacal chamber, similar to the cloacal chamber common to anus and uro-genital sinus in the Lamprey.

EXPLANATION OF PLATE 32.

Fig. 1. Cloacal region of *Myxine glutinosa* seen from the left side, ×5. The left wall of the cloaca and body-cavity has been removed. *sl.gl.* Slime-gland in upper lip of anus.

Fig. 2. Cloacal region of *Bdellostoma cirrhatum* dissected in the same way as fig. 1, ×2. The left half of the pore only is seen.

Reference Letters.

an. Anus. *cl.* Cloaca. *cl.ex.* Extension of cloaca. *fb.bd.* Fibrous band surrounding abdominal pore. *int.* Intestine buried in body-wall. *int'.* Intestine covered by peritoneum. *l.sl g.* Lateral slime-glands. *p.g.* Porus genitalis. *ur.* Ureter. *ur.p.* Urinary papilla. *mes.* Dorsal mesentery.

On the Affinities of the Madreporarian Genus *Alveopora* with the Palæozoic *Favositidæ*, together with a brief Sketch of some of the Evolutionary Stages of the Madreporarian Skeleton. By H. M. Bernard, M.A. Cantab., F.L.S.

[Read 16th December, 1897.]

(Plate 33.)

The genus *Alveopora* was founded by Quoy and Gaimard * for a coral from New Ireland collected during the voyage of the 'Astrolabe.' The original description given by these authors is intelligible and accurate so far as it goes, but the figures appear to have been drawn from memory, and certainly do not represent any known species of *Alveopora*.

The *Madrepora retepora* of Ellis and Solander, Forskål's *Madrepora dædalea*, the coral so beautifully figured by Savigny in his 'Description de l'Égypte' (tab. iii. fig. 4), and certain of Lamarck's types were soon recognized as specific forms of this new genus.

In 1848 Dana † boldly claimed the genus as belonging to the Palæozoic Favositidæ, which he classed as the second of his three

* Voyage de l'Astrolabe (Zoologie), iv. 1833, p. 240.

† 'Zoophytes,' p. 117.

families comprising the Madreporacea, this tribe being characterized by "twelve tentacles (rarely more) in one series" and lateral gemmation. According to Dana, the family Favositidæ was distinguished, on the one hand, from the Madreporidæ by the possession of tabulæ, and, on the other, from the Poritidæ by the fact that the tabulæ were replaced in these latter by spongy calcareous secretions, making the corallum everywhere equally finely porous.

This juxtaposition of *Alveopora* with the Favositidæ was rejected by Milne-Edwards and Haime, who expressed surprise * that the Alveopores, "which, in a manner, offer an exaggeration of the characters of *Goniopora* and of *Porites*, and in which the 'endotheca' is altogether rudimentary," are separated from these latter and placed at the head of a series containing *Favosites*, with its pronounced walls and numerous tabulæ. They accordingly placed *Alveopora* among the Poritidæ, while the Favositidæ are placed in a section, Madreporaria tabulata, of equal value with their other great sections, Madreporaria aporosa, Madreporaria perforata, Madreporaria tubulosa, and Madreporaria rugosa.

It is worth noting that Milne-Edwards and Haime, in thus separating *Alveopora* from *Favosites* on the ground of the tabulæ in the latter, overlooked the fact that Savigny figured his *Alveopora* from the Red Sea with tabulæ, as did also Dana his *A. spongiosa* from Fiji. Milne-Edwards and Haime made no mention of these tabulæ either in their generic or specific descriptions of the genus *Alveopora*.

In 1870, Saville Kent † reasserted the relationship between *Alveopora* and the Favositidæ, and proposed to establish a new transition genus, *Favositipora*, for a specimen of *Alveopora* with well-developed tabulæ which he found in the Paris Museum. In thus making the presence of tabulæ a generic distinction, Saville Kent followed Milne-Edwards and Haime in overlooking the tabulæ in *Alveopora*. Verrill, however, in 1872 pointed out the serious omission made by these authors, and rightly claimed Saville Kent's "*Favositipora*" as identical with *Alveopora*, but agreed with this author in claiming the genus *Koninckia*, M.-E. & H., from the Cretaceous, as a connecting link between the recent *Alveopora* and the Palæozoic Favositidæ. But, while

* "Monographie des Poritides," Ann. Sci. Nat. (3) xvi. 1851, p. 23.

† Ann. & Mag. Nat. Hist. vi. 1870, p. 386.

TUFTS COLLEGE STUDIES, NO. 5.

THE CHONDROCRANIUM IN THE ICHTHYOPSIDA.[1]

By Guy Monroe Winslow.

CONTENTS.

[1] Studies from the Biological Laboratory of Tufts College, under the direction of J. S. Kingsley, No. XIX. Reprinted from the Bulletin of the Essex Institute, Vol. XXVIII, pp. 87-141.

I wish here to give credit for some of the material used in these studies. The Necturus larvæ were given to me by Miss Julia B. Platt; for Pipa I am indebted to the late Professor E. D. Cope; Professor Robert Wiedersheim furnished me with the Protopterus material and I began the study of the chondrocranium of this Dipnoan in his laboratory. For Amphiuma I am indebted to Professor O. P. Hay, the first to find embryos of this interesting Urodele, and to the late Professor John A. Ryder, who kindly turned over to me the embryos sent him by Doctor Souchon of New Orleans. The embryo Cæcilians were given me by the cousins Paul and Fritz Sarasin and were a part of the material which formed the basis of their splendid monograph. To all these I return my best thanks.

J. S. Kingsley.

INTRODUCTION.

THE work, the results of which are given in the following pages, has been carried on in the Biological Laboratory of Tufts College, under the direction of Dr. J. S. Kingsley, to whom the author is deeply indebted, not only for the use of much of the material studied, a considerable part of which was already prepared, but far more for invaluable aid and encouragement during the preparation of this paper. It is also due to Dr. Kingsley to acknowledge the free access to his private library containing a large portion of the literature upon the subject, and to state that the models of the first stage of Amphiuma and the three stages of Necturus were made by him.

In my account of the development of the chondrocranium I have not attempted to treat of the origin of the pro-cartilage cells, but I begin with the first formation of cartilage. These earlier stages have been so ably described by Miss Platt ('93, '94) that there seems no necessity to repeat her account, especially as her discoveries in regard to the ectodermal origin of the cartilage-forming cells were largely made in this laboratory, and have received general support and confirmation in the papers of Kastschenko ('88), Goronowitsch ('92, '93, '93[a]), Klaatsch ('94, '95) and von Kupffer ('95).

One object in these investigations was to ascertain to what extent the primary cranial structures throw light upon some problems in the classification of certain Ichthyopsida. The principal of these problems were these:

(1) By most students the Cæcilians have been recognized as a distinct order of Batrachia, but more recently the late Professor Cope in several papers has maintained that these forms were in reality aberrant Urodeles and

should have only family rank in that order. Summarizing his conclusions, he maintained that the Cæcilians were descended from Amphiuma-like forms and these in turn were offshoots from some amblystomoid Urodele. The cousins Sarasin, while agreeing with Professor Cope in the view that the Cæcilians and Amphiuma were nearly related, regarded the relationship as differing in this respect. Amphiuma was a neotenic Cæcilian, a larval Cæcilian become sexually mature. My problem was to ascertain in how far the chondrocranial structures gave support to any of these views.

(2) The fact that the Dipnoi possess lungs led to the view, which has obtained wide acceptance, that these ancient fish-like forms were the ancestors of the Batrachia, and this view has received no little support from Huxley's short but most suggestive discussion of the suspensorial apparatus in the Ichthyopsida. More recently several students have maintained that the Batrachia have sprung from the Crossopterygian Ganoids and that the only relationship that can be traced between Dipnoi and Amphibians is that the lung-fishes may have had the same ancestry, but that they can in no wise be considered as in the line of batrachian descent. In how far does the chondrocranium support either of these views?

It has not been my purpose to enter the broader field of the relationships of these different groups as is shown by other features. I have confined myself closely to the chondrocranium and my results are to be regarded as merely one factor in deciding these questions; a factor in itself of minor importance.

I take as the basis of my studies the development of the chondrocranium of *Amblystoma punctata*, since of this form I have had the most abundant material. This is followed by an account of certain stages of the chondro-

crania of some other Ichthyopsida, and an attempt is made to see how far the chondrocranium can be employed as an aid in the classification of these forms.

The various stages are determined in an arbitrary manner by body length, but it is to be borne in mind that there is considerable variation in embryos and larvæ of the same size. All stages described have been modelled in wax by Born's method, the models have afterwards been carefully measured and compared and all exaggerations of proportion due to slight variations in the thickness of the wax have been corrected in the drawings.

AMBLYSTOMA PUNCTATA.

FIRST STAGE. *Embryo ten mm. long. Mouth on the point of breaking through* (Figs. 1 and 2).— This stage, which I have taken as the starting point of my investigations, corresponds closely with that at which Ph. Stöhr begins his classic account of the chondrocrania of Triton and the Axolotl ('79). The chondrocranial elements are still in the pro-cartilage condition but they are clearly differentiated from the surrounding parts by the arrangement of their cells. Three pairs of elements are present, namely, the parachordals, trabeculæ and the quadrates.

The parachordals (*p*) lie as two triangular plates upon each side of the slightly depressed anterior end of the notochord. One side of each triangular plate is directed anteriorly and the antero-exterior angle joins the posterior end of the trabecula, while the inner face of each abuts against the side of the notochord (*n*). The lateral margin of the parachordal runs obliquely outwards and forwards from its posterior angle to the junction with the trabecula. The parachordals arise separately and at this stage touch only at the sides of the notochord, thus leav-

ing the upper and under surfaces and the tip of the latter exposed.

The trabeculæ (*t*) continue forwards in nearly the same horizontal plane as the main part of the notochord, the apex of which, with the adjoining portions of the parachordals, is slightly depressed. The trabeculæ curve first outwards to a point beyond their middle and then in, their apices being about as far apart as their bases. They end medially to the olfactory organs, a little behind the external narial openings. The lower margin of each trabecula is thickened, while above it is developed into a high and thinner crest (*trc*) inclining slightly outwards. The upper margin of this crest is extremely irregular and the foramina for the optic and oculomotor nerves (*of* and *oc*) are but partially enclosed. The crest gradually increases in height from in front backwards to the posterior end of the trabecula where it terminates abruptly.

The quadrates appear as two thin bands of cartilage external to and at some distance from the parachordals. They are concave anteriorly and their general direction is downwards and outwards. In each quadrate can be already recognized three portions, a middle piece constituting a body (*bq*) from which arise an upper ascending process (*ap*) directed forward, inward and upward toward the crest of the trabecula, and a lower descending process (*dp*) running outward, forward and downward to the articulation with Meckel's cartilage. The body is somewhat lenticular while the processes are thin and more laminate.

Meckel's cartilage (*m*) is already complete. The general course of each ramus is obliquely inward and forward until about the middle point where it curves still more strongly inward to meet its fellow of the opposite side. At its base each ramus is stout but it tapers regu-

larly and is slender at the point of union. A point which seems to me of considerable morphological importance is that the symphysis is considerably behind the apices of the trabeculæ, recalling in this embryonic stage the conditions which are permanent in the Elasmobranchs and lower Ganoids.

SECOND STAGE. *Embryo, eleven mm. long* (Fig. 3).— The parts described in the first stage have chondrified rapidly and two new pairs of cranial elements, the otic capsules and the two processes of the occipital arch, have made their appearance.

The occipital arch (*ocp*) is composed of two isolated conical pieces of cartilage, the bases of which rest upon the sides of the notochord a little behind the otic region. From the notochord they curve outwards and upwards, half encircling the medulla and terminating freely. The incompletely developed otic capsules (*o*) are represented by thin layers of cartilage, very irregular in outline, covering the lateral and portions of the dorsal and ventral surfaces of the auditory vesicles. Their anterior ends lie immediately behind and above the bodies of the quadrates while their posterior ends are somewhat nearer the median line, just in front of the occipital arch. The ventral walls of the two capsules are in nearly the same horizontal plane with the notochord and the parachordals. There are no cartilaginous connections between the capsules and the rest of the chondrocranium.

The parachordals (*p*) have fused with each other at the apex of the notochord and now extend back along its sides to about the middle of the otic region where each gives off a lateral process which underlies the median portion of the sacculus. Although the median wall of the otic capsule is as yet but slightly developed, its future line of fusion with the parachordal is clearly indicated by a longitudinal marginal thickening of the latter.

Accompanying the general growth of the head and the lessening of the cranial flexure, the trabeculæ (*t*) have increased considerably in size, more especially in length. At their anterior ends they have become slightly broadened and flattened to form the cornua trabeculæ (*c*), the first indications of the nasal capsules. The gaps between the disconnected portions of the trabecular crest of the first stage are now filled, forming a plate, the dorsal margin of which is a smooth, undulating line sloping gradually downward in passing from behind forwards. The foramina for the optic and oculomotor nerves are now completely enclosed.

Several noteworthy changes have occurred in the quadrate (*q*). Its body and descending process have grown broader and thicker, and two lateral projections from the latter form a transitory support at the base of the balancer (*su*). At the time of its most complete development this support has the form of a shallow cup, the rim of which coincides with the circumference of the base of the balancer. The ascending process has extended upward and has fused with the posterior end of the trabecular crest. A slight backward projection from the body of the quadrate is the first trace of the otic process.

THIRD STAGE. *Larva twelve mm. long* (Figs. 4–7).— The distal ends of the occipital processes (*ocp*) have fused with the postero-dorsal walls of the otic capsules, and their proximal ends have fused with the posterior ends of the parachordals. A solid floor is thus formed beneath the medulla, and the jugular foramen (*j*) is enclosed by cartilaginous walls.

The parachordals (*p*) with the notochord now form a complete basilar plate below the posterior half of the brain cavity except at one small place (*f*) upon the left side which still remains unchondrified. With the excep-

tion just mentioned, the lateral margins of the parachordals are now everywhere continuous with the floors of the otic capsules.

The otic capsule (*o*) now presents the typical capsular form, covering by far the greater part of the surface of the auditory vesicle. The median wall is beginning to form along the dorsal margin and at the two ends of the capsule, leaving two unchondrified spaces in the middle and ventral region; a large anterior one through which pass the seventh and eighth nerves and the endo- and perilymphatic ducts, and a smaller fontanelle lying postero-dorsally to the first. In the floors of the capsules are the foramina for the exit of the branches of the seventh nerve (*vii*). Upon the left side the two branches of this nerve pass through the two ends of a transversely elongated foramen, while upon the right side they pass through two separate foramina formed by the fusion of the middle portions of the anterior and posterior walls of the originally elongated foramen. Behind the foramina for the seventh nerve and somewhat farther laterally is the large fenestra ovalis (*fo*). The stapes (*s*) which arises from a separate centre of chondrification occupies the anterior end of the fenestra.

The only noteworthy changes in the trabeculæ are a general strengthening and an increase in the size of the cornua (*c*). The quadrate has become more solid throughout all its parts except the processes which were at the base of the balancer in the preceding stage. They have disappeared together with the balancer, leaving a single conical process in the place they formerly occupied. The otic process (*op*) extends considerably farther backwards than before.

FOURTH STAGE. *Larva thirty-nine mm. long. Gills not yet atrophied* (Figs. 8–11).— The ventral portion of

the occipital arch is in essentially the same condition that it was in the third stage. So also are the parachordals, except that the union with the capsular floor is now complete upon both sides.

The otic capsules present several new features. From their point of fusion with the occipital processes marginal expansions (Figs. 9 and 11, *loc*) extend medially over the sides of the cranial cavity. Passing forwards they approach each other and unite to form the synotic tectum (*st*) which terminates anteriorly in a short median process (*tm*) the "tænia tecti medialis" of Gaupp. In the median wall of the capsule there are now four small apertures, of which three (Fig. 11) lie in a horizontal row near the floor of the cranium, while the fourth is more dorsal in position. Passing from in front backwards, the first foramen of the row is the one traversed by the seventh and one branch of the eighth nerve (*vii*+*viii*). The second branch of the eighth passes through the second foramen (*viii*), and the third aperture of the row is traversed by the perilymphatic duct (*pf*). The fourth aperture, higher up in the wall above the foramen for the second branch of the eighth nerve, is the foramen for the endolymphatic duct (*ef*).

At the anterior end of the otic capsule there are three new connecting cartilages joining it with the trabecula on the one hand, and on the other with the quadrate. The process joining the postero-dorsal point of the trabecular crest with the opposite wall of the capsule is relatively slender; while the other two processes, the otic (*op*) and palato-basal (*pb*), are formed by the fusion of a greater part of the dorso-median surface of the body and otic process of the quadrate with the adjacent wall of the capsule and the margin of the basilar plate. A blood vessel, which passes dorso-ventrally around the anterior end of

the capsule, is the only line of demarcation between the otic and palato-basal processes. A large chamber is enclosed between the posterior end of the trabecula, the anterior end of the capsule and the bars connecting them dorsally and ventrally. The ascending process of the quadrate passes across its external surface, separating a dorsal and a ventral foramen. The Gasserian ganglion occupies this chamber and from it pass out the ramus ophthalmicus profundus (*rp*) through the ventral foramen, and the rami ophthalmicus superficialis (*rs*), maxillaris (*rm*), and mandibularis (*rn*), through the dorsal foramen.

The foramina by which the rami of the seventh nerve leave the otic capsule are unchanged, except that now there are two upon each side and that they are considerably reduced in size. The fenestra ovalis (*fo*) is now nearly filled by the stapes (*s*), which has a slight prominence directed outwards and upwards from the antero-dorsal angle of the cartilage towards the otic process of the quadrate. These cartilages, however, do not become united at any time during the development of Amblystoma as they do in some other forms.

The trabeculæ (*t*) are of nearly uniform size from their junction with the parachordals to the point where they meet in front in the ethmoid plate (*e*). Optic and oculomotor foramina are of equal size, both being small. The ethmoid plate (*e*), arising by the fusion of the anterior ends of the trabeculæ in the median line, forms a continuous floor beneath the anterior end of the cranial cavity, the nasal septum (*ns*) and portions of the olfactory organ. In front it terminates upon each side in a conical process. Laterally a freely ending process (*c*) extends backwards along the ventral surface of the olfactory organ. This and the adjacent parts of the ethmoid plate are develop-

ments of the cornua of the earlier stages. In the same plane with the ethmoid plate and just behind its posterior end, a flat antorbital process (*anp*) projects from the side of the trabecula and, curving forwards, terminates directly behind the backward projecting process of the ethmoid plate.

A broad nasal septum rises from the middle of the ethmoid plate separating the two olfactory organs and forming the anterior wall of the cranial cavity. Bars of cartilage, which I have called the tectal cartilages (*tc*), connect the antero-dorsal points of the trabeculæ with the opposite points of the septum, roofing over the olfactory foramina and forming the bases from which curved processes, laminæ cribrosæ (*e*), extend outward, downward and forward, covering over the posterior ends of the olfactory organ.

The quadrate (*q*), besides its fusion with the otic capsule as already mentioned, now presents a well developed pterygoid process (*pt*), a cylindrical rod of cartilage joining the main part of the quadrate at the point where the ascending process meets the body. Its general direction is forwards, parallel with the trabecula as seen from above, and downwards with a slight outward curve near the tip which lies just below the ventro-median surface of the orbit.

FIFTH STAGE. *Young Amblystoma sixty-nine mm. long. Gills entirely atrophied* (Figs. 12–13).— At this advanced stage in the development of Amblystoma, ossification has occurred to so great an extent that large portions of the older cartilages have disappeared, giving the chondrocranium a broken and ragged appearance, especially in the otic region. The median capsular wall, the anterior end of the basilar plate and portions of the occipital arch, and the trabeculæ are entirely replaced

by bone. At the same time the whole skull has increased in breadth as compared to its length.

The synotic tectum (Fig. 12, *st*) is completely separated from the remnants of cartilage forming the otic capsules, and the basilar plate (*p*) is reduced in length to little more than that of the tectum. Ossification has removed nearly all of the cartilage of the capsule behind the posterior end of the fenestra ovalis where the stapes is now closely applied against the remnant of the cartilaginous wall of the capsule.

The quadrate (*q*) has undergone important changes, due in part to ossification and to the lateral expansion of the skull. Its body is thicker antero-posteriorly and stands out farther from the capsule. The descending process is cylindrical in shape, presenting greater definiteness of outline than previously. Irregular perforations of the cartilage occur along the line where the quadrate joins the capsule. Most striking of all is the change in the position of the pterygoid process (*pt*) which, instead of being nearly parallel with the long axis of the skull as in the previous stage, now slants from its base outwards at an angle of about thirty degrees from that axis.

The cartilaginous nasal capsules have reached their highest stage of development and present many new and important features. The nasal septum (Fig. 12, *ns*) is narrowed down to about half its former width. In front it divides into two doubly curved plates which extend forwards and outwards to the cup-like anterior ends of the capsules. From the ventro-median surface of each of these plates a short knob-like process extends forwards and terminates the capsule anteriorly.

A flattened band of cartilage which I have called the ventral process (*vp*), in contradistinction to the dorsal

process (*d*) to be described later, passes backwards from the ventral margin of the cup-like anterior end of the capsule. At its posterior end this process fuses laterally with the lamina cribrosa (*l*) while medially it terminates in a process projecting freely backward (Fig. 13, *vp*).

The cylindrical dorsal process (*d*) extends diagonally across the anterior end of the olfactory organ from the dorso-median margin of the cup to the anterior end of the lamina cribrosa. A short connecting rod joins the dorsal process and lamina cribrosa with the ventral process in front of the nasal duct (*nl*). As in the preceding stage, the lamina cribrosa forms a roof over the posterior end of the olfactory organ. It now reaches downwards to meet the outer end of the antorbital process thus enclosing the orbito-nasal foramen (*on*), and outwards and forwards to meet the ventral and dorsal processes as described above. It is perforated near the lateral margin by several small foramina through which pass a branch of the ophthalmicus profundus (*rp*) and some small blood vessels (*b*). A branch of the nasalis internus (*ni*) passes out of the capsule through the foramen in its median wall.

DESMOGNATHUS FUSCA (Fig. 14).

The chondrocranium of *Desmognathus fusca*, of which I have modelled two stages, presents so great a similarity to the earlier stages in Amblystoma that only a few words need be devoted to it. Figure 14 represents the model of the skull of an embryo about twenty mm. long.

The parachordals (*p*) are represented by three narrow bands of cartilage; one extending between the posterior ends of the otic capsules and having the notochord partly imbedded in it, and two other bands which connect the apex of the notochord with the posterior ends of the trabeculæ.

The entire absence of a stapes in the history of the chondrocranium is the only noteworthy point of difference between the formation of the ear capsules in Desmognathus and in Amblystoma. The trabeculæ and quadrates present conditions essentially the same as those of a corresponding stage in Amblystoma, but owing, in part at least, to the early appearance of the bony skull in Desmognathus no complex nasal capsule is formed. The simple condition shown in Fig. 14 is the highest state of development reached by the anterior ends of the trabeculæ. A small antorbital process develops in the usual place upon the side of the trabecula. No pterygoid process of the quadrate appears in either of the stages modelled. As the older stage presents a state of development approximately equivalent to that found in the fifth stage of Amblystoma the appearance of this process as figured by Wiedersheim ('77) must be a comparatively very late occurrence.

PLETHODON GLUTINOSUM (Fig. 15).

From a specimen of *Plethodon glutinosum* twenty mm. in length and showing the chondrocranium in an advanced stage of development, I have modelled the nasal capsules. In regard to the rest of the skull mention of a few points will suffice.

In the main it corresponds closely with the skull of Amblystoma as described in our fifth stage (Figs. 12 and 13). This similarity is especially noticeable in the position of the pterygoid process. There is a stapes, the antero-dorsal point of which, unlike that of Amblystoma, is connected to the quadrate by a very slender stapedial process. The otic and palato-basal processes present the usual conditions.

Aside from the rod connecting the dorsal and ventral

processes in front of the narial duct all the parts described for the nasal capsule of Amblystoma are found in approximately the same positions in Plethodon with unimportant modifications as to relative sizes. This similarity is even more apparent in older specimens of Plethodon than in the one from which this model was made. The two small foramina in the lamina cribrosa mark the points at which a branch of the ophthalmicus profundus (*rp*) enters and leaves the capsule.

NECTURUS MACULATUS.

Cope ('89) has placed *Necturus maculatus* with its American relative *Necturus punctata* and the European Proteus in a group together under the name Proteida with the remark that they occupy a position intermediate between the Stegocephali and the Urodela, and differ from the latter mainly in the possession of an intercalary bone. Descriptions of three stages in the development of the chondrocranium of *Necturus maculatus* are here given.

FIRST STAGE. — The first stage represents the skull of an embryo twenty-one mm. in length, and corresponds approximately to the condition found in Amblystoma at a time a little earlier than that represented in the third stage of the latter (Figs. 4-7). The occipital arch consists of two processes extending upward from the sides of the notochord and ending freely above. At their bases they are connected with the posterior ends of the parachordals.

The parachordals run forward from the bases of the occipital processes, slightly removed from the sides of the notochord. Between the posterior ends of the otic capsules they bend inwards and touch the sides of the notochord to which they are attached for a short distance, then curve sharply outward, and, fusing laterally with the cap-

sular floors, continue forward into the trabeculæ. The notochord projects forward some distance in front of the most anterior point at which the parachordals touch its sides. The otic capsules are widely separated and incompletely formed. Their floors are partially attached to the parachordals and the only traces of the median wall are found around the inner margins of its walls. A large fenestra ovalis, with no stapes, and a large foramen for the exit of branches of the seventh nerve constitute the only well defined apertures which are found in later stages.

The trabeculæ extend forwards from the anterior ends of the parachordals as long slender rods running parallel for the posterior three-fourths of their length and then bending inward at an angle of about thirty degrees towards the median line, which they do not reach. There are, as yet, no foramina for the second and third nerves and only a slight trace of a trabecular crest to which the ascending process of the quadrate is attached.

The quadrate is wedge-shaped as seen either from the side or in front, the point being directed ventrally. A short otic process extends upward and backward from the dorso-lateral angle of the wedge and fuses with the otic capsule, while a longer ascending process extends upward and forward from the dorso-median angle and fuses with the dorsal end of the slightly developed trabecular crest.

SECOND STAGE. — Our second model is that of an embryo twenty-four mm. in length. The occipital processes are fused distally with the walls of the otic capsules and continue along the dorso-median angles of the capsules as the beginnings of the synotic tectum. The jugular foramen is at this stage a dorso-ventrally elongated slit.

In place of the distinctly outlined parachordals of the previous stage we now have a continuous basilar plate

lying beneath that portion of the cranial cavity included between the posterior halves of the otic capsules. As before, the notochord projects freely forward in the median line. Laterally and in front the basilar plate merges into the capsular floors and the trabeculæ.

The otic capsules present essentially the same conditions found in stage three of Amblystoma (Figs. 4–7) except that the otic process of the quadrate is fused with the antero-ventral surface of the capsule. A trabecular crest just large enough to enclose the optic and oculomotor foramina and to form a point of attachment for the ascending process is now developed. The appearance of simple antorbital processes upon the sides of the trabeculæ is the only further change which needs mention here.

THIRD STAGE. *Larva forty-five mm. long* (Fig. 16). — A continued fusion of the margin of the occipital process with the wall of the otic capsule, resulting in a reduction of the size of the jugular foramen, is the most noticeable change in this region. The synotic tectum is now fully developed and presents the usual form. The basilar plate remains the same as in the previous stage.

The otic capsules have reached their highest state of development. The median wall is perforated by four foramina which correspond almost exactly to those described for the otic capsule of the fourth stage of Amblystoma (Fig. 11). In fact the only differences of any importance between the otic regions of this skull and that described as the fourth stage for Amblystoma are in the absence of the parachordals at the anterior end of the notochord, and the more median position of the foramen for the palatine nerve (*pal*). A small crest is now developed along the posterior half of the trabecula. A slender connecting rod unites the posterior end of the crest with the opposite wall of the otic capsule. Antorbital processes project outward and forward from the sides of the trabeculæ.

By a fusion of the anterior ends of the trabeculæ in the median lines a small ethmoid plate is formed, upon the anterior end of which is a slight prominence, the only indication we have of a nasal septum. Upon each side a short forward-projecting process terminates the ethmoid plate anteriorly.

Entirely separated from the rest of the cartilaginous parts of the head there is now a delicate nasal capsule (Fig. 16, *nc*). It consists of a curved rod, which runs along the dorso-median surface of the olfactory organ, following more or less closely the direction of the anterior end of the trabecula and the ethmoid plate, and a number of shorter processes projecting laterally from this main rod over the top of the olfactory organ. As Pinkus ('94) has pointed out, there is some resemblance between this nasal capsule and that of Protopterus, but it seems to me hardly necessary, for reasons which will appear more fully later, to attach any importance to this similarity other than that of a coincidence.

One would seem justified in expecting that, if Necturus occupy a position intermediate between the Stegocephali and the Urodela, the chondrocranium of Necturus would show more or greater differences from the typical Urodele chondrocranium than are found in higher Urodeles, the Urodela of Cope. But I am unable to discover that this is the case. It would be difficult, rather, to point out a form in which the chondrocranium is more typically Urodelan.

AMPHIUMA MEANS.

The first of the two models of the chondrocranium of *Amphiuma means* here described is the one which formed the basis of the description of the chondrocranium in Dr. Kingsley's preliminary paper upon "The Head of an Embryo Amphiuma" ('92). The chondrocranium of

another specimen from the same lot of embryos was also described and figured by Professor O. P. Hay in his paper of '90.

FIRST STAGE (Figs. 17–18).—The occipital processes have fused with the otic capsules and their distal ends project inward over the sides of the cranial cavity as the first steps in the formation of the synotic tectum. The parachordals (Fig. 18, *p*) extend forward from the bases of the occipital processes, and, after curving inward to the sides of the notochord and fusing beneath it, they each divide into a median and a lateral band. The lateral bands of the two sides curve outward and, fusing with the capsular floors, pass forward to the posterior ends of the trabeculæ. The median bands separate in front of the apex of the notochord, bend laterally and join the lateral bands again at their junction with the trabeculæ. Between these two parts of each parachordal a fontanelle is enclosed.

The otic capsules present nearly the same condition as that found in the fourth stage of the skull of Amblystoma. But here, as was also noted in Necturus, the foramen for the palatine branch of the seventh nerve (*pal*) is on the median side of the median capsular wall.

The trabeculæ extend from their union with the parachordals forward to the nasal region, where they fuse in a small ethmoid plate which is terminated anteriorly by two broad triangular cornua. Along the middle and posterior end of each trabecula is a well-developed crest covering in the optic and oculomotor foramina as usual. It is connected postero-dorsally with the anterior end of the otic capsule, and it is also connected with the median angle of the quadrate by means of the ascending process (*ap*). The point at which the ascending process joins the trabecula is relatively farther anterior in Amphiuma than in Amblystoma, thus producing more elongate foramina for the exit

of the nerves coming from the Gasserian ganglion (Fig. 18, *v*). Antero-dorsally the crest gives rise to a rod of irregular shape, which projects forward, outward and downward. This is the lamina cribrosa (*e*). Below and a little behind this the antorbital process is just beginning to appear upon the side of the trabecula.

The quadrate is rhomboidal in outline when viewed from the side. It is connected with the trabecular crest by the ascending process, as mentioned above, but as yet it has not fused with the otic capsule. From its posterior angle a slender stapedial process (Fig. 17, *sp*) extends backward into the anterior end of the fenestra ovalis where it joins the small stapes. No pterygoid process is yet developed. Meckel's cartilage articulates with the antero-ventral surface of the quadrate.

SECOND STAGE (Fig. 19).—In the second stage of the chondrocranium of Amphiuma, ossification is far advanced. The most important additions to the cartilages are seen in the completed nasal capsule and the pterygoid process (*pt*) of the quadrate which is now developed.

The distal ends of the occipital processes have developed into a narrow synotic tectum, while the notochord and median portions of the parachordals have disappeared except in the occipital region, where they form a ventral band (*p*) connecting the two capsules. No changes worthy of notice have taken place in the otic capsules aside from the results of ossification.

The trabeculæ are divided into anterior and posterior portions by ossification in the orbital region. The posterior portion remains essentially the same as in the first stage, but the anterior portion is changed by the formation of the nasal capsule. The base of the antorbital process (Fig. 19, *anp*) marks the posterior end of that portion of the trabecula remaining unossified in front of

the optic foramen. A narrow column of the trabecular crest projects upwards from just in front of the base of the antorbital process, and upon the anterior end of the ethmoid plate a thin nasal septum is developed. Two cartilages upon each side arise from the dorsal end of the septum. From its posterior end a cylindrical rod, the tectal cartilage (*te*) extends backward and outward to the dorsal point of the remnant of the trabecular crest. From the posterior end of the septum a band of cartilage extends forward and expands into a broad sheet, the nasal tectum, roofing over the whole anterior portion of the olfactory organ. Where the nasal duct passes out to the exterior (*nl*) at the anterior end of the tectum, a complete ring of cartilage encircles it. Laterally the nasal roof is connected by a band curved ventrally with the cornu (*c*) of the trabecula. And from the postero-lateral margin of the tectum a flattened rod (*l*) passes backward to the tectal cartilage, fusing with it at a point just above the anterior end of the antorbital process.

While it is impossible to homologize all the parts of the nasal capsule of Amphiuma with those in Amblystoma there are some points in which the similarity between them is very close. The septa, ethmoid plates, and tectal cartilages are essentially alike in both. The lamina cribrosa and dorsal process of Amblystoma are represented in Amphiuma by the rod connecting the tectal cartilage with the nasal tectum. The open anterior end of the capsule of Amphiuma is quite different from the cup-like end of Amblystoma to which it must be compared. This difference in the capsules is, of course, correlated with the relative change of position of the nostrils, which are at the anterior end of the capsules in Amphiuma and in the middle of the sides of the capsules in Amblystoma. In Amphi-

uma the antorbital process does not become fused with the lamina cribrosa.

The quadrate is now supplied with a pterygoid process (*pt*) which runs forward from the ventral surface of the ascending process in close proximity with the ventral margin of the trabecula. Towards its anterior end it curves laterally and broadens out into an oval plate. Its anterior end lies a short distance postero-laterally from the base of the antorbital process. Otic and palato-basal processes unite the quadrate with the otic capsule. The stapes has expanded into a broad plate nearly filling the fenestra ovalis. It is still connected with the quadrate by a strong stapedial process (*sp*).

CHARACTERISTICS OF THE URODELE CHONDROCRANIUM.

From the preceding descriptions of the chondrocrania of various Urodeles, we may briefly enumerate the more important characteristics of the cartilaginous skull as found in this group.

Two occipital processes, the early history and relationships of which have been more fully treated by Ph. Stöhr ('79), arise independently at the sides of the notochord in front of the first permanent vertebra. The similarity between these processes and those of which the vertebræ are formed clearly indicates the vertebral nature and origin of the occipital arch. From the sides of the notochord the occipital processes pass upward, fuse with the walls of the otic capsules and bend over medially to form the synotic tectum (Fig. 18, *ocp*). Two large jugular foramina are enclosed between the bases of the occipital processes and the posterior ends of the otic capsules. Parachordals, varying in size and extent from the narrow bands of Desmognathus (Fig. 14, *p*) to the complete

basilar plate of Amblystoma (Figs. 9 and 10 *p*), form a more or less complete floor beneath the otic portion of the brain cavity. The otic capsules are approximately oval in shape and in all cases have a median wall distinctly separating the cavity of the capsule from that of the brain. There are generally four foramina in this wall through which pass the seventh and eighth nerves and the endolymphatic and perilymphatic ducts. In the ventro-lateral wall of the capsule there is a large fenestra ovalis which may or may not be occupied by a stapes. When present the stapes appears first at the anterior end of the fenestra and only later, if at all, does it reach back to the posterior wall of this aperture. The stapes may be connected with the quadrate by a stapedial process.

Trabeculæ, either slender rods with barely enough crest to cover in the optic and oculomotor foramina as in Desmognathus, or solid beams as in Amblystoma, connect the parachordals and otic capsules with the nasal capsules. At its posterior end there are two places at which each trabecula joins the cartilages of the otic region. Of these points of fusion, the ventral, joining the base of the trabecula with the parachordal, is formed early, while the dorsal, joining the trabecular crest with the otic capsule, is a later occurrence. Anteriorly the trabeculæ usually bend inward, and, fusing in the median line into an ethmoid plate, take part in the formation of somewhat complex nasal capsules. But here, again, Desmognathus, with nothing more complex than cornua trabeculæ (Fig. 14, *c*), proves an exception to the general rule.

An antorbital process projects outward and forward from the side of the ventral margin of the trabecula behind the olfactory organ. In some forms it later fuses with the other parts of the nasal capsule. The variety of forms shown by the nasal capsules of the different

species described renders it difficult to make any accurate statements in regard to these organs which shall apply to the group as a whole. More extended study may show the prevalence of a limited number of these types as is suggested by the similarity between Amblystoma and Plethodon.

Quadrates, arising independently near the anterior end of the otic capsules, later become attached to the rest of the skull by three or four processes. The ascending process unites it with the trabecular crest; the palato-basal with the parachordal; the otic with the otic capsule; and the stapedial process, when present, unites it with the stapes. The palato-basal and otic processes become so intimately related that the blood vessel running between them is the only line of demarcation. A pterygoid process running forward from the body of the quadrate may or may not be present. When present it ends freely in front, not coming in contact with the anterior end of the trabecula and nasal capsule as occurs regularly in the Anura. Ranodon forms the only known exception among the Urodeles to this last statement.

PIPA AMERICANA (Figs. 20–21).

In the single stage of the chondrocranium of Pipa which I have modelled, ossification has proceeded so far that many of the cartilages appear only as remnants of what they were earlier. A brief outline of this skull, however, may serve as a basis from which, with the aid of other studies upon the Anura, especially Gaupp's exhaustive work upon *Rana fusca*, we may contrast the chondrocranium of this group with that of the Urodela.

The occipital processes have fused with the otic capsules and their distal ends have developed into the synotic

tectum. The parachordals are reduced to a narrow transverse band immediately in front of the base of the occipital arch, and short lateral bands fused with the floors of the otic capsules. The greater part of the wall of the otic capsule is ossified, but enough of the lateral wall remains to show the most important relationships. In this lateral wall of the capsule, further dorsally than in the Urodele skull described, is the fenestra ovalis and in it a small stapes (Fig. 20, *s*) which is connected by a rod running forward and downward with the lateral border of the tympanic annulus (*ta*).

The trabeculæ are small, cylindrical rods extending forward from the ventro-median angles of the anterior ends of the otic capsules and fusing in the broadly expanded ethmoid plate. In the median line the ethmoid plate is continued forward into the nasal septum. At the sides of the posterior end of the septum the ethmoid plate is perforated by the olfactory foramina (*ol*). A triangular lamina cribrosa (*l*) projects outward, downward and forward from each antero-lateral margin of the ethmoid plate. This and the septum with the connecting rods compose the nasal capsules.

From the ventro-lateral margin of the lamina cribrosa (Fig. 21) a slender cartilage projects horizontally inward to beneath the inner border of the lamina where it splits into two cylindrical rods, a dorsal and a ventral. The dorsal rod (*d*) extends forward inward and upward to the antero-dorsal point of the septum, while the ventral rod (*vp*) curves sharply inward, touches the ventral margin of the septum and then, slightly expanding in width, terminates in a process projecting freely forward. A small foramen for the orbito-nasalis, seen only when the skull is viewed from below (*on*), passes beneath the posterior end of the lamina-cribrosa just outside the anterior end of the

trabecula. The short so-called 'palatine cartilage' is, as has been shown by Gaupp, the homologue of the antorbital process of the Urodela.

The quadrate is situated much nearer the posterior end of the skull than that of the Urodela described. It lies about under the middle of the lateral wall of the otic capsule, to which it is connected by means of a dorsal otic and a ventral palato-basal process. There is no stapedial process connecting the quadrate directly with the stapes, but, as was mentioned above, the stapes is connected with the tympanic annulus which is earlier derived from the quadrate. A slender palato-pterygoid process (*ppt*) projects forward from the body of the quadrate and fuses with the lateral margin of the lamina cribrosa. The relatively posterior position of the quadrate adds proportionately to the length of Meckel's cartilage.

ANURA AND URODELA CONTRASTED.

From a general view of the chondrocrania of these two groups it is seen that, on the whole, in the Anura the width is greater in proportion to its length than in the Urodela. But since there are many very short and broad skulls among the Urodela this distinction is of little value. The closure of the cranial cavity is more complete in the Anura, especially in the ventral region where the basicranial fontanelle, as shown by Gaupp ('93), becomes greatly reduced. Here, too, instead of ending freely, the pterygoid process of the quadrate is attached anteriorly to the ethmoid plate. In these two last mentioned points the Anura show more resemblance to the Selachians than do the Urodela.

We may here insert a few words in regard to the homologies and terminology of the cartilages which have

been variously called the 'antorbital process' and the 'palatine cartilage.' Gaupp ('91) maintained the homology of the 'antorbital' of the Urodela with the palatine of the Anura. Speaking of this cartilage in Amphiuma, Kingsley ('92) said, "the lower process may retain the name, antorbital, usually applied to it, for Amphiuma presents no evidence that it is the palatine cartilage as Gaupp interprets it." In his final paper on the chondrocranium of Rana, Gaupp ('93) repeats his former position and, stating that he uses the two terms interchangeably, comments upon the above quotation as follows: "Kingsley scheint unter 'Palatine Cartilage' hier etwas Besonderes zu verstehen; was das ist, kann ich aus seinen Angaben nicht ersehen."

There seems to be no doubt as to the correctness of the homology of the cartilages as pointed out by Gaupp. The question here, however, is one of terminology and it is not to be settled by the fact that certain authors have called this cartilage the palatine, but upon the broader grounds of comparative anatomy, and here the question of priority must also be taken into account. The term palatine bone in some of its various modifications was first applied to a bone occurring in the palatal region of the Mammalia, and, in transferring the name to other classes of vertebrates, it is obligatory that it should be given only to those structures which are homologous with the palatine of mammals. That the palatine *bone* of the Amphibia is homologous with the palatine bone in the mammals I do not deny, but I maintain that this cartilaginous process is in no way a palatine process but that rather its relations are with the nasal capsule, and for the following reasons:

In the mammals the palatine bone is regularly enumerated among the membrane bones (Minot '92, *inter alia*) and, so far as I am aware, it has no connection with any

cartilage. To attempt to homologize a membrane bone with a cartilage is a difficult task. If, however, it be maintained that we have here a case of substitution such as exists in the roofing bones (parietals, frontals, etc.) of the cranium, in which the cartilaginous roof of the brain cavity becomes replaced by the immigration of dermal bones, Ichthyophis throws considerable light upon the question. In this form the palatine bone (part of the maxillopalatine process of the Sarasins), which is distinct in early stages, arises, not in connection with the cartilaginous process in question, but with the nodule of cartilage shown in Figs. 22, 23, and 24, *pc*. In Ichthyophis not only is this true cartilaginous 'palatine' present but the antorbital process occurs as well.

If we adopt the usually accepted homologies (which, however, are not beyond question) the palatine of the higher vertebrates is to be sought in the anterior portion of the upper jaw of the Elasmobranchs, which is accordingly called the palato-pterygo-quadrate or some similar term, implying homologies with the palatine of higher forms. In these very Elasmobranchs, however, the exact homologue of this antorbital process exists, in no way connected with the upper jaw but rather as forming a part of the nasal capsule.

The transformation during metamorphosis from a condition in which the jaw of a small suctorial mouth articulates with the anterior end of the pterygoid cartilage to one in which it reaches back to the body of the quadrate beneath the middle of the otic capsule is one of the most striking characteristics of the Anuran chondrocranium. Another of its distinctive features is found in the auditory apparatus. While in the Urodela the fenestra ovalis may be occupied by a cartilaginous stapes which may or may not be connected with the quadrate by a stapedial process,

in the Anura we find a much more complicated condition. The fenestra ovalis passes through important changes of form and the stapes comes into connection with a tympanic annulus. But if the tympanic annulus was "originally a postero-superior leaf cut off from the mandibular suspensorium," as stated by Parker and Bettany ('77), the fundamental similarity of the conditions in the two groups is apparent. In connection with this point Gaupp says, "Der vom Quadratum losgelöste knorpelige Annulus tympanicus scheint eine dem Anuren allein zukommende Bildung zu sein." Here, as with the Urodela, the nasal capsule offers little that is of classificatory value.

The chief points of difference between the chondrocranium in the two groups may be tabulated as follows:

URODELA.	ANURA.
1. Both broad and narrow types.	1. Generally, if not always, broad.
2. Pterygoid free in front (except in Ranodon).	2. Pterygoid attached to ethmoid plate.
3. Basi- and supra-cranial fontanelles large.	3. Basi- and supra-cranial fontanelles smaller.
4. No metamorphosis.	4. Very striking metamorphosis.
5. Auditory apparatus comparatively simple.	5. Auditory apparatus, including the tympanic annulus, complex.

ICHTHYOPHIS GLUTINOSUS.

FIRST STAGE (Figs. 22 and 23).—The specimen from which the model for this stage was made was a young embryo still spirally coiled within its membranes. While in some places, more particularly toward the anterior end of the head, the tissue modelled is not true cartilage, the differentiation of all the parts is sufficient to cause little difficulty in distinguishing them.

The notochord occupies its usual position at the posterior end of the cranium; but, as it passes forward, it bends downward so that its anterior end lies considerably below the general level of the cranial floor. The parachordals are represented only by a narrow band of cartilage connecting the posterior ends of the otic capsules. In the median line the notochord is embedded in this band. At its lateral margin the parachordal band fuses with the occipital process behind and with the otic capsule in front. The dorsal end of the occipital process is fused with the otic capsule. Between these three cartilages is the jugular foramen (*j*).

The otic capsules are longer, narrower and deeper than those of Amblystoma, and, as is usual in the younger stages, they are comparatively widely separated. In the median wall of each capsule are two foramina, a larger anterior and a smaller posterior foramen. The ventrolateral wall of the capsule is largely taken up by the fenestra ovalis along the dorsal part of which lies the stapes. The stapes is continued forward into a process which reaches the posterior surface of the quadrate. This process may retain the name 'stapedial process,' although in this case it is continuous with the stapes rather than with the quadrate. The stapes is perforated in a dorso-ventral direction for the arteria perforans stapedia (Fig. 23, *as*).

Three processes arise from the anterior end of the otic capsule. Two of these, which I shall call the dorsal (*dr*) and ventral (*vr*) trabecular rods, extend forward in the usual positions of the dorsal and ventral margins of the trabecula. The third, and relatively much shorter process is attached posteriorly to the otic capsule just below the end of the dorsal trabecular rod. Curving downward and forward it fuses with the ventral trabecular rod. In the posterior end of the ventral trabecular rod there is a small

foramen traversed by a nerve (apparently the palatine). This foramen does not appear in the later stages modelled but I am unable to give the details of the disappearance.

After passing forward separately to the orbital region, the dorsal and ventral trabecular rods of each side are connected by two narrow bands of cartilage, a post-orbital (*pob*) and a pre-orbital (*prb*) between which the elongated optic foramen (*of*) is enclosed. Beginning in the region of the post-orbital band the dorsal and ventral trabecular rods of each side, which have thus far been approximately parallel, diverge in a horizontal direction. The dorsal rod curves first outward and then inward, giving off ventrally a plate-like lamina cribrosa near its anterior end. The two ventral rods bend inward to the median line where they unite to form a small ethmoid plate. Just behind their point of fusion each ventral rod gives off a ventro-lateral process which underlies the posterior end of the olfactory vesicle. From the anterior margin of the pre-orbital band of cartilage an antorbital process (Fig. 23, *anp*) extends outward and forward towards the ventral portion of the lamina cribrosa.

The quadrate is composed of a body, and ascending and pterygoid processes. The body is small and stands out from the side of the ventral trabecular rod below the anterior end of the ear capsule, with which it is not directly connected. The ascending process passes upward and forward and unites with the dorsal trabecular rod a little in front of the ear capsule. The pterygoid process (*pt*) is composed of two parts, a short proximal portion which projects forward from the body, and an isolated portion which later becomes the distal end of the process. This method of development of the pterygoid is the same as that mentioned by Gaupp ('91) for Siredon. A short dis-

tance in front of the distal portion of the pterygoid is another isolated rod of cartilage which runs in a direction diagonal to that of the pterygoid process. This is the palatine cartilage (*pc*).

Meckel's cartilage articulates with the ventral surface of the body of the quadrate. Anteriorly the cartilages of the two sides are still separated. They project backward behind the point of articulation with the quadrate nearly as far as the posterior end of the stapes (*a*).

SECOND STAGE (Figs. 24–26).—The parachordals and occipital processes are in the same condition as before, there being no trace of the formation of a synotic tectum. The notochord has entirely disappeared from the head region. The median wall of the otic capsule is more complete than it was in the first stage (Fig. 25). What was then the large anterior foramen is now divided into a dorsal foramen for the endolymphatic duct (*ef*) and a large ventral foramen for the auditory and facial nerves. The floor of the capsule is now composed of a median and a more lateral rod between which a fontanelle is enclosed. The stapes and fenestra ovalis are in the same condition as in the preceding stage.

The rod described in the first stage as connecting the anterior end of the otic capsule with the ventral trabecular rod now has a nearly vertical direction, the ventral end being relatively more posterior in position than before. As far forward as the orbital region there are no other noteworthy changes. In the nasal region, however, important changes have occurred. Instead of the transversely expanded nasal region of the earlier stage, we now find the anterior ends of the dorsal trabecular rods folded inward toward the nasal septum and forming a roof over the sides of the olfactory organs. By this movement the

lamina cribrosa is brought into its usual position. Its distal end is fused with that of the antorbital process thus enclosing the orbito-nasal foramen (Figs. 24 and 26, *on*).

The ethmoid plate is larger in both directions than in the first stage, and in the median line upon its anterior half arises the nasal septum (*ns*). In front, upon the sides of the base of the septum, the ethmoid plate terminates in short free processes. The nasal septum is divided anteriorly into three parts, a short median process which projects freely forward, and two lateral bands which curve forward and outward. At its most anterior point each of these bands divides into a dorsal and a ventral process. These extend backward along the lateral surface of the olfactory organ and fuse with the outer end of the cartilage mentioned in the first stage as arising from near the anterior end of the ventral trabecular rod. Where these three processes meet a plate of cartilage is formed which lies below the lamina cribrosa and is connected with it by a short narrow band. No tectal cartilage is formed in the chondrocranium of Ichthyophis.

As a result of ossification the ascending process of the quadrate has lost its cartilaginous connection with the dorsal trabecular rod (Fig. 24), and the parts of the pterygoid process are now united into one continuous rod. The body of the quadrate remains essentially unchanged, it having neither otic nor palato-basal process. The two cartilages of Meckel are now confluent in front, and the palatine cartilage still remains isolated from the rest of the chondrocranium. It appears that the ancestors of the Batrachia had a palato-pterygo-quadrate cartilage similar to that found in sharks. Of these cartilages the Urodeles as a rule retain only the pterygoid and quadrate portions. The Cæcilians have these two parts and an isolated palatine portion, while in the Anura all three parts are united

in one rod which is joined in front to the antorbital process.

THE CÆCILIAN CHONDROCRANIUM.

There are two views according to which the Cæcilians are related to Amphiuma. According to one — the theory of Cope ('89[a]) — the Cæcilians are the extreme of a line of degeneration from the typical Urodele stock and Amphiuma is one of the intermediates of the series nearest to the Gymnophiona. Indeed, Cope goes so far as to make the Cæcilians merely a family of the Urodeles. The other view is that of the cousins Sarasin who hold that Amphiuma is a neotenic Cæcilian, a larval Cæcilian become sexually mature while retaining their branchial respiration.

According to the first view Amphiuma, and to a less extent the rest of the Urodeles, must be closely similar in cranial as well as other structures to the young Cæcilian. Farther, if we find that Amphiuma and the Urodeles have lost certain features which belonged to the ancestral Craniota, the retention of these characters by the Cæcilians would be an argument against the line of descent advocated. The view of the Sarasins presents even more difficulties for we have both horns of the dilemma. If Amphiuma be merely a Cæcilian arrested in a larval condition, then we have to say either that Amphiuma is not related to the remaining Urodeles or that they have all sprung from a Cæcilian ancestry. The objections to the second view are so many and so weighty that we think no one would care to defend it. The limbs alone are enough to set it aside. As to the other horn, it would seem that all the evidence we have regarding adult structure and development as well goes to show that Amphiuma is far more closely allied to the other Urodeles than it is to the Cæcilians, while the same matter of limbs, weak though

they be in Amphiuma, throws the whole view out of court.

There remains then but the view of Cope, and this is to be tested by seeing if there be features in the Cæcilians which must have been inherited and which could not have been inherited from an Urodele ancestor.

The parachordals of Ichthyophis are smaller than those of any other form studied. The nearest approach to them is found in Desmognathus where there are bands, not present in Ichthyophis, connecting the anterior end of the notochord with the otic capsules. No synotic tectum is formed in Ichthyophis, though at one period in the development of the skull small crests on the dorso-median walls of the otic capsules represent the first steps in the formation of a tectum. This appearance, however, is slight and but transitory.

There is a difference between the manner of development of the trabeculæ of Ichthyophis and those of the other Batrachia described. Instead of being developed by the successive formations of a ventral rod, a trabecular crest and a connective rod uniting the crest to the otic capsule, we have the dorsal rod developing simultaneously with the ventral rod and equally well chondrified. The dorsal rod, separated as it is from the ventral rod and attached to the anterior point of the otic capsule, somewhat resembles the supraorbital band of fishes. But the fusion of the ascending process of the quadrate with the dorsal rod and the relations of the two trabecular rods anteriorly are clearly Urodelan characters. The quadrate is peculiar, however, in having no otic or palato-basal processes. Aside from the ascending process and stapes it is entirely separated from the rest of the skull. Its position is the same as that of the Urodeles. The stapes is perforated for the stapedial artery.

But more important than any of the features mentioned above is the existence of an isolated palatine cartilage. This is especially noteworthy since it seems to furnish strong evidence in opposition to the theory of the Urodelan ancestry of the Cæcilians. Ranodon is the only Urodele which possesses that portion of the palato-pterygoid arch which may be considered to correspond to the palatine cartilage of Ichthyophis, while in Amphiuma there is not the slightest trace of it. We may therefore conclude that the condition found in Ichthyophis was not derived from an Urodelan ancestor but from some more primitive form.

The articular process of Meckel's cartilage is unusually long in Ichthyophis. The nasal capsules, while differing from all the others described, have no features of sufficient importance to be of any especial classificatory value.

The evidence which I have found, chiefly from a study of the chondrocranium, appears to me to be against associating the Cæcilians with any of the Urodeles and in favor of keeping them in a distinct group coördinate with the Urodela and Anura.

POLYPTERUS BICHIR (Fig. 27).

In 1892 the late H. B. Pollard kindly allowed Dr. Kingsley to trace the outlines of the cartilages in the sections of the head of his youngest Polypterus. From these drawings I have made the chondrocranium in wax. Since the skull of this same specimen has already been described and figured by Pollard ('91) I shall deal chiefly with points of value from a comparative standpoint. For further details in regard to the relations of the chondrocranium to the rest of the head, reference should be made to Pollard's paper which contains a

dorsal view of the skull and drawings of sections through various parts of the head.

No cartilaginous occipital arch is present, owing, apparently, to ossification. The otic capsule is large and selachian-like in form. In its postero-lateral wall there is a large aperture exposing portions of the posterior and horizontal canals. This also is probably due to ossification. A small remnant of the hyomandibular cartilage (*h*) lies in a groove in the dorso-lateral surface of the capsule. That it formerly reached down as far as the posterior end of the pterygo-quadrate cartilage is shown by the figures of Pollard and others.

A thick synotic tectum covers the brain cavity in the posterior two-thirds of the otic region. There are indications of a medial capsular wall separating the brain cavity from the cavity of the capsule at its posterior and anterior ends, but the greater part of the space is entirely open. The floors of the capsules are continuous with the básilar plate which slightly exceeds the synotic tectum in extent. A peculiar rod of cartilage (*bo*) projects a short distance backward from beneath the middle of the basilar plate. At the anterior end of the capsules there are upon each side two foramina and a deep groove which is now open in front and apparently represents another foramen the anterior wall of which is ossified. A short bar of cartilage passes across the external opening of the posterior of the two foramina, dividing it here into two. The unossified posterior end of the supraorbital band remains as a solid lateral projection upon the anterior end of the otic capsule.

There is a complete separation of the chondrocranial elements of the otic region from those of the orbital and nasal regions. The supraorbital band (*sb*) passes anteriorly into a broad tegmen cranii (*tc*) which covers over

the anterior end of the cranial cavity and continues forward into the roof of the nasal capsules. Ventrally a solid plate of cartilage (*t*), the trabecular plate, forms a continuous floor beneath the anterior end of the cranial cavity and the nasal capsules, and projects forwards as a short and rather blunt rostrum (*r*). A small isolated plate of cartilage (*tc*) occupies the middle of the supracranial fontanelle, a remnant, as Pollard suggests, of a primitively complete tegmen cranii.

The nasal capsule consists of a large cavity enclosed by simple, broad plates of cartilage. Its floor and roof are connected by a tall septum medially and two bands laterally. The posterior of these two bands marks the boundary between nasal capsule and cranial cavity. There are three large apertures in the capsule walls: behind, the olfactory foramen; in front, the foramen for the nasal duct (*nl*); and between them a third in the lateral wall. Besides these there are two small foramina in the border of the nasal roof, the 'canalis ethmoidalis' (*ec*) and the 'canalis preorbitalis' (*prc*). Dorsally these two are connected by a deep groove.

The anterior end of the palato-pterygo-quadrate cartilage (*ppt*) is applied to the ventro-lateral surface of the nasal capsule. From here it passes backward as a broadening band to a point beneath the outer wall of the otic capsule and the hyomandibular cartilage. In passing from in front backward it twists from an approximately horizontal to a nearly vertical plane.

THE TROUT (*Salmo fontinalis*), (Figs. 28–29).

For a representative of the Teleostean skull I have modelled the chondrocranium of a trout embryo twenty-two mm. in length. The occipital arch is fused with the

otic capsules leaving no suggestion of their former separation, except in the jugular foramina (Fig. 29 *j*). The notochord extends forward beyond the middle of the otic region. Its sides are embraced by the two halves of the basilar plate. At its apex it projects freely forward for a short distance. Except for a small fontanelle (*f*), the basilar plate is continuous with the walls of the otic capsules which are united above by a broad, arched synotic tectum. The positions of the semicircular canals are clearly indicated in the external surface of the otic capsules. No median wall separates the cavity of the ear from that of the brain. In front and a little below the jugular foramen there is another smaller foramen through which the ninth nerve (*ix*) passes out of the cranium. Farther forward there are three more apertures in the ventral wall of the capsule. The posterior of these is the fontanelle mentioned above. The middle one of the three is small and is traversed by the hyomandibular branch of the facial nerve (*hy*). The anterior foramen is for the exit of a branch of the jugular vein (*jv*).

The basilar plate is continued forward into a trabecula upon either side. These extend separately to a point in front of the hypophysis and then unite along the median line in a narrow trabecular band. This band has the shape of an inverted trough and reaches to the anterior end of the skull, expanding in the nasal region into the ethmoid plate which forms the floor of the nasal capsules. The palatine branch of the seventh nerve (Fig. 28, *pal*) passes downward through a foramen in the posterior end of the trabecula. Two slender supraorbital bands (*sb*) arise from the anterior ends of the otic capsules and curve forward and inward, until about half way from the otic to the nasal region, where they enter the margins of the arched tegmen cranii which covers the anterior end of the

cranial cavity. This cranial roof is fused anteriorly with the dorsal end of the nasal septum (Fig. 28, *ns*). In its anterior end there are three apertures, a median fontanelle and two small lateral foramina, through each of which passes a branch of the ophthalmicus superficialis (*rs*). A band of cartilage connecting the tegmen cranii and the dorsal end of the septum with the lateral border of the ethmoid plate separates the nasal region from the cranial cavity. There is no cartilaginous roof or lateral wall to the nasal capsule. The septum is thick and slightly expanded dorsally and in front where it ends bluntly.

The anterior end of the pterygo-quadrate cartilage is applied to the ventro-lateral margin of the ethmoid plate. From here it extends backward as a slender rod to beneath the anterior end of the otic capsule where it broadens into an irregular plate with an articular process ventrally for the attachment of Meckel's cartilage. Its posterior end is connected with the otic capsule by means of the plate-like hyomandibular cartilage (*h*). The dorsal margin of this cartilage, the hyomandibular, lies closely pressed against the external surface of the otic capsule just beneath the horizontal canal. It is broad and thin above and narrower and thicker below. From its ventral end a long rod-like process runs forward beneath the posterior end of the pterygo-quadrate, reaching almost to the point of articulation with Meckel's cartilage. The hyomandibular branch of the seventh nerve passes through a foramen just above the middle of this cartilage (*hy*).

THE CHONDROCRANIUM IN THE FISHES.

The chondrocrania of the two types of this group which have been described have many features in common, and it seems probable that a comparison of corres-

ponding stages in the development of the two forms would show a still more marked similarity. The otic capsules are connected dorsally by a solid synotic tectum and ventrally by an unbroken basilar plate formed by the fusion of the parachordals around the anterior end of the notochord. The median wall of the otic capsule is either absent or but slightly developed. Neither fenestra ovalis nor stapes occurs.

The trabeculæ unite ventrally into a median band in front of the hypophysis and continue forward to the end of the skull. At its anterior end the trabecular band broadens out into the ethmoid plate which forms the floor of the nasal capsules. Supraorbital bands extend forward from the anterior ends of the otic capsules to the lateral margins of the tegmen cranii which roofs over the anterior portion of the brain cavity.

The palato-pterygo-quadrate cartilage extends from the lateral margin of the ethmoid plate backward to beneath the anterior end of the otic capsule. Its posterior end is supported to a greater or less degree by the ventral end of the hyomandibular cartilage which has its dorsal end closely applied against the outer wall of the otic capsule. Meckel's cartilage articulates with the ventral surface of the quadrate portion of the palato-pterygo-quadrate cartilage.

In discussing the relations of Polypterus to the Batrachia, Pollard said, "On comparing the primordial cranium of a young Polypterus with that of Urodeles, the general resemblance is seen to be so great that an anatomist seeing it alone for the first time would certainly place it among the latter." Considering the features which distinguish the chondrocranium of Polypterus in common with the rest of the Fishes from that of the Batrachia, as outlined in the preceding pages, so great a similarity can

hardly be admitted to exist. The great similarity pointed out above between the skulls of Polypterus and the trout and the many points in which they differ from the typical skull of the Batrachia cause me to feel considerable hesitancy about accepting the theory of the Crossopterygian ancestry of the Batrachia. But, while the presence in Polypterus of a large hyomandibular cartilage, a quadrate well removed from the otic capsule and a strong supraorbital band, as well as the absence of any fenestra ovalis or stapes, will remain important obstacles to this view until transitional stages are found, perhaps these difficulties are less than those attending the Dipnoan theory. Attention may also be called to the fact that in Polypterus there is a limited median capsular wall, which is not found in either the trout or Protopterus but which regularly occurs in the Batrachia.

PROTOPTERUS ANNECTENS (Figs. 30–32).

A model of the chondrocranium of Protopterus gives us a basis from which to compare the Dipnoi on the one hand with the Batrachia, to which they have been considered to be closely related, and on the other to the Teleosts and Ganoids.

Viewed as a whole the massive character of many of the cartilages of this skull is a most striking feature. Ossification in the occipital region somewhat obscures the relations between the skull and the first vertebra. The occipital processes are fused with the otic capsules leaving large jugular foramina in the usual position. The remnant of the notochord is imbedded in a solid parachordal plate extending from the posterior end of the skull forward to the middle of the otic region. On each side of the median line at the anterior end of the parachordal plate is an

elongate fontanelle (Fig. 32, *f*). The walls of the otic capsules are continuous ventrally with the parachordal plate and dorsally with a strong synotic tectum. From the external margin of the otic capsule a broad ledge of cartilage projects horizontally outward, widening as it passes from behind forward where it terminates abruptly. There is no median capsular wall.

Band-like trabeculæ extend forward along the sides of the brain from the dorsal anterior end of the otic capsules to the optic region where they bend around ventrally to form a large ethmoid plate. From the dorsal margin of the anterior end of each trabecula a peculiarly bent antorbital process (*anp*) arises. It projects forward and outward, coming into close proximity to, but not fusing with the posterior end of the nasal capsule, and then it bends backward, running along the margin of the upper lip. The ethmoid plate narrows down in passing from behind forward, and terminates in two processes which bend sharply upward and fuse with the posterior end of the nasal septum. Between these two terminal processes there is an oval fontanelle.

The nasal capsule is a very peculiar one. The septum is a thin dorsal plate behind, but in front it becomes a solid cylindrical mass of cartilage projecting ventrally between the olfactory organs. The transition from one condition to the other is very abrupt. In front the septum ends in two short laterally directed processes. Six bands of cartilage extend outward and downward from the median septum to a curved marginal band (*mr*). Between these bands five apertures of various shapes and sizes are enclosed. The anterior of the six transverse bands projects somewhat beyond its point of fusion with the marginal band. As is seen in the ventral view (Fig. 32) a curved process extends inward and upward from the inner

border of the marginal band. Its dorsal end is free. Just in front of the bend of the antorbital process is an isolated strip of cartilage occupying a diagonal position, one end being dorso-medial and the other ventro-lateral. A small cylindrical rod (*tc*) extends backward in the median line from the posterior end of the nasal septum and ends freely above the brain, a remnant of the ancestrally complete tegmen cranii.

The quadrate has its base firmly fused with the otic capsule and trabecula. It is a solid mass projecting downward and forward, and presents upon its anterior end a large articular surface for the enormous posterior end of Meckel's cartilage (Fig. 30). Except for a short distance in front of its point of articulation, Meckel's cartilage is of only ordinary size. There are upon each side of the lower jaw three labial cartilages (*lc*). As shown in the figure the posterior of these is separated from the jaw and divided into two parts, but this occurred upon the right side only. By mistake the anterior end of the lower jaw was drawn nearly straight instead of curved sharply upward as it should have been.

The ninth nerve (*ix*) passes out through a small foramen a short distance in front of the jugular foramen. Five foramina grouped about the anterior end of the otic capsule open upon the dorso-lateral surface of the skull. I have designated the nerves passing through these foramina in accordance with the work of Pinkus ('94). The third nerve passes through a small foramen (Fig. 30, *oc*) near the dorsal margin of the trabecula. Just below the foramen for the third is a larger one for the ramus ophthalmicus profundus of the fifth (*rp*), and still lower is another for the ramus maxillaris of the fifth (*rm*). A short distance behind this foramen are the openings of the other two lying close together, one above the other. The

more dorsal of the two is traversed by two nerves, the ramus lateralis facialis of the seventh (*rl*) and the ramus ophthalmicus superficialis of the fifth (*rs*). The more ventral foramen is for a blood vessel (*b*).

Three foramina open upon the ventral surface of the skull in this same region (Fig. 32). Of these the anterior and smallest is for the ramus palatinus superior (*rps*). The other two openings are close together. The more median is for the main trunk of the seventh (*vii*) and the ramus palatinus inferior (*rpi*). The more lateral opening is the ventral end of the foramen for the blood vessel mentioned above.

THE CHONDROCRANIUM IN THE DIPNOI.

A comparison of the chondrocranium of Protopterus with those of the Batrachia and Fishes at once reveals its unique character. While resembling the typical chondrocranium of each of these groups in some respects, taken as a whole it is very different from either. The large otic capsule, with thick walls and separate foramen for the ninth nerve, and without a median wall or fenestra ovalis, greatly resembles the capsule of Fishes. But the suspensorial apparatus is entirely different from that of most Fishes and very similar to that of the Batrachia, that is to say, it is autostylic. According to Huxley ('76) this condition is also found in the Chimæroids and Marsipobranchii, but in none of the other Fishes. This is undoubtedly the strongest point of resemblance between the chondrocrania of the Dipnoi and Batrachia. And here the theory of the Dipnoan ancestry of the Batrachia is decidedly at an advantage over the Crossopterygian theory. But this similarity of the otic relations of the quadrate in these two forms is counterbalanced by differ-

ences in other respects. The absence of a palato-pterygoid cartilage is an especially noteworthy feature in this connection which indicates the highly specialized nature of this skull and renders it impossible to consider it a very near approach to the ancestral Batrachian skull.

The trabeculæ are unlike both those of the Fishes and those of the Batrachia. When their posterior ends are compared with the chondrocranium of the former group they seem rather to represent the supraorbital bands, arising as they do from the antero-dorsal surface of the otic capsules. But in passing forward, instead of curving up over the eye as supraorbital bands should do, they curve downward and fuse at their anterior ends into an ethmoid plate very much as occurs in the Batrachia. The antorbital process arises from the dorsal margin of the trabecula, a condition found in none of the other forms studied; and the ethmoid plate, instead of continuing forward to form a floor beneath the nasal capsules, as is the general method in both Fishes and Batrachia, curves sharply upward at its anterior end and fuses with the dorsally situated posterior end of the nasal septum. The possession of a remnant of the tegmen cranii is another fish-like character.

As was mentioned in the discussion of the chondrocranium of Necturus, there is some resemblance between the nasal capsules of that form and those of Protopterus. But, in view of the differences between the nasal capsules of the various forms of Urodeles themselves and considering the many important points of difference in other parts of the skull, it seems to me an entirely unwarrantable conclusion to assume any phyletic relationship between these two forms upon this account.

Günther has described the skull of Ceratodus as consisting "of a completely closed inner cartilaginous

capsule and an outer incomplete osseous case, to which, again, some other cartilaginous elements are appended." From this description and from the fact that a cartilage considered to be a remnant of the hyomandibular has been found in Ceratodus it seems probable that the chondrocranium of this form resembles that of the Fishes more than does that of Protopterus. But the evidence from the chondrocranium of Protopterus, in so far as it may be considered to have value in determining the position of the Dipnoi as a whole, appears to me to be entirely in agreement with the conclusion of W. N. Parker that, "it is certainly inadvisable to retain the Dipnoi among the Fishes, as is still done by some zoologists, and it would be still more undesirable to place them with the Amphibia." It is to be remembered, however, that Protopterus is one of the more specialized forms of the group.

POSTSCRIPT.

Since the foregoing article passed into the hands of the printer a paper by Miss Platt[1] has appeared which deals with the development of the cartilaginous skull of Necturus, giving special attention to the origin of the procartilage cells. In the main our results in regard to the fully chondrified parts entirely agree. Miss Platt finds, however, that in Necturus the number of cartilages arising independently is considerably larger than that described above for Amblystoma. Of these the synotic tectum ('tectum interoccipitale'), the trabecular crest, and the ethmoid ('internasal') plate are of particular interest

[1] Platt, J. B. The development of the cartilaginous skull and of the branchial and hypoglossal musculature in Necturus. Morph. Jahrbuch. XXV, p. 377. 1897.

from the fact that I have not found them to appear as independent cartilages in any of the forms studied. This may, in some cases, be due to the fact that the independent condition is limited to the pro-cartilage stages or to the incompleteness of my series of embryos. But I feel confident that the parts mentioned do not appear as independent cartilages in Amblystoma. The existence of such a condition as that shown in Fig. 18, where there is no sign of cartilage near the median line, and the appearance of a complete tectum in an embryo but little older form the basis of my conclusions in regard to the synotic tectum. My evidence as to the formation of the trabecular crests and the ethmoid plate is of the same nature and shows them to be outgrowths from the primitive trabeculæ.

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EXPLANATION OF THE FIGURES.

REFERENCE LETTERS.

a. Angular process.
a n p. Antorbital process.
a p. Ascending process.
a s. Arteria perforans stapedia.

b. Foramen for blood vessel.
b o. Basi-occipital cartilage.
b q. Body of quadrate.

c. Cornu trabeculæ.

d. Dorsal nasal process.
d p. Descending process of quadrate.
d r. Dorsal trabecular rod.

* Not seen

e.	Ethmoid plate.
e c.	Ethmoid canal.
e f.	Endolymphatic foramen.
f.	Fontanelle.
f o.	Fenestra ovalis.
h.	Hyomandibular cartilage.
h y.	Foramen for hyomandibular branch of seventh nerve
i x.	Foramen for ninth nerve.
j.	Jugular foramen.
j v.	Foramen for branch of jugular vein.
l.	Lamina cribrosa.
l c.	Labial cartilage.
l o c.	Lateral occipital crest.
m.	Meckel's cartilage.
m r.	Marginal rod.
n.	Notochord.
n c.	Nasal capsule.
n i.	Foramen for branch of nasalis internus.
n l.	Nostril.
n s.	Nasal septum.
o.	Otic capsule.
o c.	Oculomotor foramen.
o c p.	Occipital process.
o f.	Optic foramen.
o l.	Olfactory foramen.
o n.	Orbito-nasal foramen.
o p.	Otic process.
p.	Parachordal.
p a l.	Palatine foramen.
p b.	Palato-basal process.
p c.	Palatine cartilage.
p f.	Perilymphatic foramen.
p o b.	Postorbital band.
p p t.	Palato-pterygo-quadrate cartilage.
p r b.	Preorbital band.
p r c.	Preorbital canal.
p t.	Pterygoid process.
q.	Quadrate.

r.	Rostrum.
r l.	Foramen for ramus lateralis facialis of the seventh nerve.
r m.	Foramen for ramus maxillaris of fifth nerve.
r n.	Foramen for ramus mandibularis of fifth nerve.
r p.	Foramen for ramus ophthalmicus profundus of fifth nerve.
r p i.	Foramen for ramus palatinus inferior.
r p s.	Foramen for ramus palatinus superior.
r s.	Foramen for ramus ophthalmicus superficialis of fifth.
s.	Stapes.
s b.	Supraorbital band.
s p.	Stapedial process.
s t.	Synotic tectum.
s u.	Support of balancer.
t.	Trabecula.
t a.	Tympanic annulus.
t c.	Tegmen cranii.
t e.	Tectal cartilage.
t m.	Taenia tecti medialis.
tr c.	Trabecular crest.
v.	Foramen for branch of fifth nerve.
vii.	Foramen for branch of seventh nerve.
viii.	Foramen for branch of eighth nerve.
v p.	Ventral nasal process.
v r.	Ventral trabecular rod.

EXPLANATION OF PLATES.

Fig. 1. Side view of model from *Amblystoma punctata*, ten mm. long.

Fig. 2. Dorsal view of same.

Fig. 3. Dorsal view of model from *Amblystoma punctata*, eleven mm. long.

Fig. 4. Side view of model from *Amblystoma punctata*, twelve mm. long.

Fig. 5. Dorsal view of same.

Fig. 6. Ventral view of same.

Fig. 7. Dorso-median view of otic capsule of same.

Fig. 8. Side view of model from *Amblystoma jeffersoniana*, thirty-nine mm. long.

Fig. 9. Dorsal view of same.

Fig. 10. Ventral view of same.
Fig. 11. Median view of otic capsule of same.
Fig. 12. Dorsal view of model from *Amblystoma punctata*, sixty-nine mm. long.
Fig. 13. Ventral view of same.
Fig. 14. Dorsal view of model from *Desmognathus fusca*, twenty mm. long.
Fig. 15. Dorsal view of model of nasal capsules from *Plethodon glutinosum*, twenty mm. long.
Fig. 16. Dorsal view of model from *Necturus maculatus*, forty-five mm. long.
Fig. 17. Side view of model from young *Amphiuma means*.
Fig. 18. Dorsal view of same.
Fig. 19. Ventral view of model from older *Amphiuma*.
Fig. 20. Dorsal view of model from *Pipa americana*.
Fig. 21. Ventral view of nasal region of same.
Fig. 22. Dorsal view of model from young *Ichthyophis glutinosus*.
Fig. 23. Ventral view of same.
Fig. 24. Side view of model from older *Ichthyophis glutinosus*.
Fig. 25. Median view of otic region of same.
Fig. 26. Dorsal view of nasal capsules of same.
Fig. 27. Side view of model from young *Polypterus bichir*.
Fig. 28. Side view of model from trout twenty-two mm. long.
Fig. 29. Ventral view of same.
Fig. 30. Side view of model from young *Protopterus annectens*. (See text, p. 190, for error in shape of Meckel's cartilage.)
Fig. 31. Dorsal view of same.
Fig. 32. Ventral view of same.

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6

THE DEVELOPMENT OF THE TYMPANO-EUSTACHIAN PASSAGE AND ASSOCIATED STRUCTURES IN THE COMMON TOAD (BUFO LENTIGINOSUS).

BY HENRY FOX.

A perusal of the literature relating to the subject reveals the existence of considerable diversity of opinion among investigators as to the exact morphological significance of the tympano-Eustachian passage of the higher vertebrates. So far as its adult structure and relations are concerned, the passage would seem to be the homologue of the spiracle or hyomandibular cleft of the elasmobranch fishes. Both structures occupy the same relative position between the mandibular and hyoid arches, and, moreover, above the dorsal margin of each the facial nerve divides into its two main branches, one of which, the ramus palatinus, courses in front of the cleft (or tube, as in the higher forms), while the other, the ramus hyomandibularis, extends ventrally along its posterior wall. Embryologists, however, in studying the development of the tympano-Eustachian passage in various species of the higher vertebrates, have found that its homology with the hyomandibular cleft is not so clearly expressed as the mature structure of the organ would lead one to infer, so that certain morphologists, basing their conclusions on the facts revealed by embryology, hold that the tympano-Eustachian passage is a structure entirely, or in large part, independent of the hyomandibular cleft.

In order to determine, if possible, the exact relation of the tympano-Eustachian passage to the hyomandibular cleft, I undertook to follow out its entire embryonic history in the common toad of the eastern United States, *Bufo lentiginosus*.[1] Contributions to the knowledge of the development of the structures under consideration had been made in the case of the *Anura* by Goette,[2]

[1] The investigations have been made in the Zoological Laboratory of the University of Pennsylvania.

[2] *Entwicklungsgeschichte der Unke, Bombinator igneus*, Leipzig, 1875.

Villy,[3] and Gaupp.[4] Shortly after I had begun the present research a very important paper on the subject by Dr. Hans Spemann appeared, treating of the earlier stages in the development of the Eustachian tube in *Rana temporaria.*[5] All the investigators mentioned state that the development of the tympano-Eustachian passage in the forms studied is a very indirect one and that it can be traced only with considerable difficulty. This difficulty is attributed to the almost complete atrophy of the hyomandibular cleft, which at an early period becomes so greatly reduced as to be readily overlooked unless special attention is bestowed on it.

Of the investigators mentioned Goette correctly described the degeneration of the hyomandibular cleft, but his other results concerning the development of the Eustachian tube may be disregàrded, since his investigations were conducted at a time when less favorable methods were at his disposal than we have at present. From the results arrived at by the other three investigators a fairly complete history of the Eustachian tube may be made out in the case of *Rana temporaria.* Of these the work of Villy covers fairly well the period of the metamorphosis, although his descriptions are somewhat inexact,[6] and his conclusion, that the Eustachian tube "has almost certainly nothing to do with the hyomandibular cleft," and that "the evidence offered by the frog tends to show that the two organs have no connection whatever with each other," is certainly unsound, since such a connection between the two has been established by the very careful work of Spemann on the earlier stages of the tube in the same species. The correctness of Spemann's conclusions are corroborated by the results which I have obtained in *Bufo.* Gaupp's chief contribution consists in his calling attention to the appearance of the tubal *Anlage* at a stage earlier than that in which it was first observed by Villy. For further information concerning the results arrived at by these investigators the reader is referred to the papers mentioned.

[3] "The Development of the Ear and Accessory Organs in the Common Frog, Rana temporaria," *Quar. Jour. of Micros. Sci.*, 1890.

[4] "Beiträge zur Morphologie des Schädels, I, Primordial-cranium von Rana fusca," *Morph. Arb.*, V, 2, 1893.

[5] Spemann, "Ueber die erste Entwicklung der Tuba Eustachii und des Kopfskelets von Rana temporaria," *Zoologische Jahrbücher*, 1898.

[6] As, for instance, he speaks of the tube as extending forward beneath the palato-pterygoid bar, which it never does, but, instead, passes beneath the quadrate. Moreover, his figures show it in the latter position.

I. Observations and Results.

I now turn to the description of the development of the tympano-Eustachian passage in the common toad. In this undertaking I shall first treat in detail the condition and relations of the structures under consideration in the different stages, beginning with the earliest, and then at the end of the paper summarize the chief features of this development.

Stage I (Pl. VI, fig. 1).—I begin at a stage when the hitherto almost spherical embryo has elongated and when the tail has grown out as a short stump. No external gills are as yet apparent. The head has become differentiated from the body proper and the region immediately posterior to it is marked by two or three slight dorsi-ventral grooves, indicating the position of the future branchial-clefts.

Pl. VI, fig. 1 is a coronal section of the anterior portion of an embryo of this stage. The section is slightly oblique, the right side being cut at a higher plane than the left. In this figure one will notice that the anterior extremity of the pharynx is still separated from the exterior, the conjoined endoderm and ectoderm forming at this point a solid partition of cells—the stomatodeal plate (*st.*). From this region posteriorly the cavity of the pharynx gradually widens out until it forms a spacious chamber, the sides of which are marked by four dorso-ventral grooves, marking the inner openings of the visceral-clefts. Just back of the fourth visceral-cleft the cavity narrows very suddenly to form the lumen of the œsophagus.

As shown by the figure, there are only four visceral-clefts (*Hym.*, 2–4 *v.f.*) marked out at the present stage. With the exception of the fourth, each of the clefts extends outward as a solid, double-layered plate of endoderm, continuous at its inner end with the epithelial lining of the pharynx and externally in contact with the deeper layer of the ectoderm. Only the medial portion of each cleft shows a lumen. The fourth visceral-cleft resembles the others, except that it does not as yet quite reach the epiblast.

[6] In the drawing the distal extremities of the clefts are shown separated by a narrow, clear area from this layer, but this condition, I think, must have been produced by shrinkage, a supposition which receives support from the rough and irregular character of the distal edge.

Between the visceral-clefts intervene the visceral-arches. The interior of each arch is made up of a mass of rather compact mesenchyme, consisting of scattered cells, containing numerous large yolk-spheres, barely distinguishable from those occurring in the endodermic lining of the pharynx. From this circumstance the limits of the endoderm are somewhat difficult to define clearly, and accordingly considerable care had to be taken in outlining it. The endoderm is, however, much more densely crowded with yolk-spheres and hence appears as a darker layer more or less clearly marked off from the surrounding lighter mesenchyme. Four visceral-arches are clearly differentiated, the two anterior of which are the mandibular (*k.m.*) and hyoid (*h.m.*) arches, while the other two are the first and second branchial-arches. In the former two a somewhat dense patch of mesenchyme can be seen occupying the centre of each. These patches are the *Anlagen* of the future muscles of these arches (*k.m.* and *h.m.*).

An examination of the remaining sections of the series to which fig. 1 belongs, shows that the pharyngeal cavity retains approximately the same size throughout its entire dorso-ventral extent and that throughout their entire length the visceral-clefts have about the same direction and relations as shown in the figure. Hence we may look upon the clefts as being solid folds of endoderm, compressed antero-posteriorly and elongated dorso-ventrally. Throughout their entire extent the first three clefts are apparently in contact with the deeper layer of the ectoderm.

The first or hyomandibular cleft resembles the other clefts in all essential respects, except that it extends slightly forward whereas the second extends transversely outward, while the remaining two course obliquely backward. A section of the cleft in almost any coronal plane presents the condition shown in the figure. Immediately dorsal to the outer extremity of the cleft the distal portion of the facial ganglion becomes continuous with the deeper or sensory layer of the ectoderm.

Stage II (Pls. VI, VII, figs. 2–7).—In this stage all five visceral-clefts are present, none of which opens to the exterior. The mouth is still separated from the pharynx by the stomatodeal plate. The external gills have budded forth as two minute, blunt, undivided processes from the sides of the first and second visceral-arches.

In specimens of the present stage the *Anlagen* of the various structures have so far differentiated that they are in most cases readily recognizable. The mesenchyme is less compact than hitherto. The *Anlagen* of the muscles are particularly well marked out as prominent patches of densely aggregated mesenchyme cells, containing numerous yolk-spherules. The blood-vessels also have begun to form in the head region.

Pl. VI, figs. 2, 3 and 4 are coronal sections of a tadpole of this stage. Of these fig. 2 was taken at a plane a slight distance above the floor of the pharynx. Comparing it with fig. 1 we find that anteriorly the stomatodeal invagination (*st.*) has deepened very considerably, although as yet not communicating with the pharyngeal cavity. The latter has much the same form as in fig. 1, except that posteriorly an additional visceral-cleft is present. Of these clefts the most anterior, the hyomandibular (*Hym.*), can be seen as a narrow, solid diverticulum of the pharyngeal wall, extending outward and terminating bluntly in the mesenchyme a short distance below the external ectoderm. All the remaining cleft outgrowths reach to and blend with the external ectoderm, although as yet not opening to the exterior. Within the body of each of the two anterior visceral-arches—*i.e.*, mandibular and hyoid—the muscles can be made out as irregularly defined patches of denser mesenchyme. That in the mandibular arch is the *Anlage* of the muscles of mastication (*k.m.*), while that in the hyoid arch is the *Anlage* of the depressor mandibulæ + depressor ossis hyoidei [7] (*h.m.*). Anterior to the first cleft is a small vessel, the mandibular aortic arch (*m.a.*), while on the left of the figure another vessel is to be seen posterior to the cleft. The latter is the hyoidean aortic arch (*h.a.*).

Pl. VI, fig. 3 is taken at a considerably higher level. On the right side we have passed above the dorsal margins of the visceral-clefts, so that the latter are shown only on the left side. This section passes in a plane approximately on a level with the base of the brain, the small dark patch in the median line in front of the pharyngeal cavity being the floor of the infundibulum (*inf.*). The hyomandibular fold can be seen extending outward and slightly forward. It will also be noticed that its distal [8] end approaches the

[7] Spemann includes these two muscles under the term "orbito-hyoideus."

[8] A word of explanation is necessary concerning my use of the terms "distal" and "proximal." Ordinarily these terms are used only in connection

skin more closely than in fig. 2. In fig. 4 we see the fold at its dorsal origin from the pharyngeal wall (*Hym.*). Here it is to be seen as a rather wide, shallow, blunt diverticulum of the latter. In the sections intervening between this and fig. 3 the distal end progressively moves peripherally as we pass down until it comes to occupy the position shown in the latter figure. Hence the dorsal edge of the cleft is higher in its proximal portion than in its distal part. In fig. 4 it will also be noticed that the proximal portion of the cleft in its dorsal portion approaches very closely to the origin of the second visceral-cleft. In the other two figures the cleft is separated throughout by a considerable interval from the second cleft. It follows from this that as it descends the plane of the first cleft moves forward also.

Grouping the facts so far obtained we find the hyomandibular cleft as a solid, two-layered diverticulum of the pharyngeal wall, which extends outward and somewhat forward to a point a short distance removed from the external ectoderm. Here it terminates in a blunt, rounded edge, extending downward and slightly forward and presenting throughout its course no well-marked indentations or depressions. Above and below, however, the outer edge gradually recedes more and more from the skin until it blends imperceptibly with the lining of the pharyngeal cavity. The edge thus has the form of a gentle arch. In general the cleft outgrowth is elongated dorso-ventrally, but it also is directed obliquely forward. This forward direction is more pronounced in its dorsal than in its ventral portion. In its lower portion the cleft is widely separated from the second visceral-cleft, but in its dorso-posterior portion it approaches the latter very closely, particularly in its proximal, internal part.

These observations are further confirmed by transverse sections (Pls. VI, VII, figs. 5–7). In fig. 5 the hyomandibular cleft can be seen as a short, blunt diverticulum from the inferior, outer angle of the pharynx (*Hym.*). The cleft here is cut through its antero-

with processes or appendages of the body. In the present paper, however, I designate by "distal" that portion of the hyomandibular fold (or of its derivative, the Eustachian cord) which is farthest removed from its connection with the pharynx, while I employ the term "proximal" to denote that part of the same structure which is nearest the point of origin from the pharynx. My use of these terms in connection with the structure mentioned is due to the necessity of having some fixed term to apply to each of its extremities, the relative position of which vary in the different stages.

ventral portion. In the fifth section posterior to this (fig. 6) the cleft is cut throughout the greater part of its dorso-ventral extent, and hence appears as a broad, solid mass extending out from the side of the pharynx and reaching nearly to the skin, where it all but meets a slight papilla projecting inward from the latter (*Hym.*). This figure also reveals another feature of the cleft-outgrowth which is of particular importance. It will be noted that it is the upper portion of the cleft-fold which approaches most nearly the skin, whereas the ventral portion recedes gradually from it as we descend. About the middle of this ventral portion is a small indentation in the outer edge occupied by a small blood-vessel (*x.*). It will be also noticed that the proximal (inner) portion of the cleft is situated at a higher level than in fig. 5. From this it follows that the line of origin of the fold from the pharynx extends from below upward and backward.

Posterior to this region the hyomandibular fold bends more sharply backward and accordingly in transverse section appears considerably narrower (fig. 7, *Hym.*, right side). We next obtain the condition shown in fig. 5 (left side), where the fold (*Hym.*) is cut approximately at right angles to its surface and hence appears extremely narrow. Below the fold is a large oval mass, the *Anlage* of the hyoidean muscles, *i.e.*, depressor mandibulæ and depressor ossis hyoidei (*h.m.*). Spemann has noticed a relation between the subsequent development of these muscles and the degeneration of the hyomandibular fold. I have found the same relation to exist in *Bufo*, but shall call attention to it later. The fold next enlarges somewhat, and then, gradually receding more and more from the exterior, blends imperceptibly with the pharyngeal wall. These stages are shown consecutively in figs. 6 and 7 (left sides).

The transverse sections also show some structural features, which are of importance in tracing certain stages in the subsequent history of the cleft-fold. Anterior to the cleft is the efferent mandibular aortic artery, a branch from the carotid. At the present stage this vessel is rather difficult to trace, but with some care can be worked out. Since, owing to the general antero-ventral direction taken by the plane of the hyomandibular fold, the anterior wall of the latter faces forward and also upward, it follows that in transverse section structures anterior to the fold will be seen dorsal

to it. Thus in the figures the region immediately dorsal to the fold is the mandibular arch, whereas that ventral to it is the hyoid arch. In fig. 7 the efferent portion of the mandibular aortic arch can be seen as a transversely placed vessel (*m.a'.*) just above the roof of the pharynx and extending outward above the hyomandibular diverticulum. Internally the vessel unites with the carotid (*car.*). The course of the mandibular aortic arch can be followed by comparing the figures. At first it is very small, as seen in fig. 5 (*m.a'.*). Tracing it forward, however, it is soon found to be continuous with a much larger vessel with a well-marked lumen. This vessel is the afferent portion of the mandibular aortic arch (*m.a''*). Immediately beneath the antero-inferior extremity of the hyomandibular fold the mandibular aortic arch is joined by the hyoidean aortic arch, and the common trunk thus formed communicates with the large inferior jugular sinuses beneath the mouth.

The other structure to which I desire to call attention is the hyomandibular ramus of the facial nerve. The facial ganglion at present lies just back of and above the dorsal margin of the hyomandibular fold. The anterior edge of the ganglion is in actual contact with the outer margin of the fold (fig. 7, *vii*). From the ventral surface of the ganglion the hyomandibular ramus (fig. 6, *vii h.*) is given off as a large nerve supplying the muscles of the hyoid arch. It is hence posterior to the hyomandibular fold.

Stage III (Pls. VII, VIII, figs. 10–14, 16–18).—Young tadpole. External gills prominent and considerably branched, not covered as yet to any marked extent by the opercular fold. Third visceral-cleft opening to the exterior. Mouth communicating with pharynx. The tail has attained its full development.

A considerable departure from the conditions observed in the preceding stage is shown in the present. The different organs are quite clearly differentiated, while the *Anlagen* of the more important cartilages can be made out as dense aggregations of the mesenchyme. The first visceral-cleft especially has undergone marked modifications. We can follow out its course by comparing figs. 10–14. Consulting fig. 10, we notice that the pharyngeal wall is separated from the exterior by a considerable interval occupied by scattered mesenchyme cells, which in the region immediately surrounding the pharynx are segregating to form the *Anlagen* of the

skeletal structures. Since it will be necessary hereafter in studying the development of the Eustachian tube to take into consideration the modifications undergone by the neighboring skeletal parts, it may be well to point out these parts in the present stage. The very dense segregated mass which may be seen in fig. 10 (*M.* and *Q.*), immediately external to and beneath the pharynx, is the *Anlage* of the cartilaginous mandibular arch. That portion of the arch which underlies the pharynx is the mandibular or Meckel's cartilage (*M.*), while that external to it is the quadrate or suspensorium (*Q.*). In the figure there is no distinct separation between these two portions, but more anteriorly the mandibular *Anlage* can be seen to be separated from the quadrate by a slight space in which the mesenchyme cells are less densely aggregated (fig. 11, *M.*—shown here owing to the oblique section, the left side being cut more anteriorly than the right). In fig. 10 (*M.*) only the most posterior part of the mandible can be seen. The mandible, as in all anuran tadpoles, extends transversely beneath the floor of the mouth. External to the lateral wall of the pharynx (right side) is the quadrate cartilage (*Q.*), which ventrally becomes continuous with the mandible and at the same point sends upward and outward a strong process, the orbital process or processus muscularis (*Pr.M.*) (Gaupp). This process with the inner portion of the quadrate forms a deep concavity, underlying the eye and containing the muscles of mastication. That portion of the quadrate which lies in contact with the pharyngeal wall is the palato-pterygoid process or commissura quadrato-cranialis anterior of Gaupp (fig. 11, *Pr.q.c.a.*). At its dorsal extremity this part approaches, but is still separated from, a patch of dense tissue in immediate contact with the dorso-lateral border of the pharynx, the *Anlage* of the trabecula cranii (*Tr.*).

On the right side of fig. 11 (fourth section posterior to that of fig. 10), the mandibular cartilage has been passed, and in its stead we find a very slight aggregation of mesenchyme forming a portion of the cartilaginous hyoid bar. The trabecula cranii of the same side has become much less distinct, and in the third section following (fig. 12) has ceased to be any longer distinguishable from the surrounding mesenchyme. The trabeculæ cranii at present are thus marked out only in their more anterior portion. Of the quadrate cartilage we have only the body with its processus mus-

cularis, having passed beyond the transversely placed commissure quadrato-cranialis anterior (palato-pterygoid). Of the quadrate the outer, distal portion of the processus muscularis is most distinct at the present stage. Above this process are the muscles of mastication (*k.m.*) already mentioned, while to its outer or ventral surface are attached two muscles, the depressor mandibulæ (*m.d.m.*) and depressor ossis hyoidei (*m.d.h.*). Between these two muscles courses the ramus hyomandibularis of the facial nerve (*vii h.*). Both of these muscles belong to the hyoid or second visceral-arch and have been differentiated out of the common muscle mass of that arch.

The quadrate in the region posterior to that just considered blends gradually and imperceptibly with the surrounding mesenchyme. This can be followed by examining the figures consecutively.

We will now turn to the consideration of the hyomandibular fold in the present stage. In fig. 12 the rhomboidal cavity of the pharynx is sharply prolonged at its right ventro-lateral angle, and from the wall of the cavity immediately above this prolongation a narrow, solid cord, representing an extension of the wall, extends upward and outward in close contact with the ventral surface of the processus muscularis (*Eu.*). Just internal to its blind, distal extremity can be seen a small vessel interposed between the cord and the cartilage. This vessel is the mandibular aortic arch. Ventral to the cord is a semicircular mass of procartilage, in the hollow of which is placed the depressor mandibulæ. This is the *Anlage* of the hyoid, a more complete view of which can be obtained in fig. 13 (*H.*). The hyoid, like the mandible, is a stout, thick bar placed transversely beneath the floor of the pharynx and separated from its fellow in the mid-line by a less compact tissue. Anteriorly the two are separated by the thyroid gland outgrowth (*Th.*). At its outer extremity the hyoid turns sharply upward as a flattened plate with a concave outer surface in which is lodged, as already mentioned, the depressor mandibulæ. Its inner surface is closely applied to the outer and ventral wall of the hyomandibular fold (*Eu.*).

In the region posterior to that shown in fig. 12 the hyomandibular fold presents much the same appearance as in the last stage (compare figs. 13 and 14 with 6 and 7). It will be noticed, how-

ever, that the fold is considerably narrower than in the preceding stage, and also that its distal extremity is much farther removed from the external surface. This condition will be more fully considered presently. The narrowing of the fold, however, is more apparent than real. If one will bear in mind the statement already made that the fold extends downward and obliquely forward, a true explanation of the difference will suggest itself. Naturally a section which passes through in the same plane as that of the fold will show the latter as a broad mass. This explains the appearance of the fold as shown in fig. 6 (right side). In this figure the section on the right side passes through the eye, whereas on the left side it passes some distance behind the eye. Hence the section traverses the right side in an obliquely forward direction, thus coinciding in the main with the plane of the fold. In the same specimen the fold on the left side is cut throughout transversely, so that, except in its most posterior portion, it appears as a narrow, two-layered lamina.

It is in its distal anterior portion that the hyomandibular fold has undergone its greatest modification. In fig. 12 the fold is continuous with the wall of the pharynx. In fig. 11, which is the third section anterior to that of fig. 12, this connection no longer exists. The fold appears as a solid, somewhat flattened cord (*Eu.*), closely underlying the upper, outer extremity of the processus muscularis. Its internal surface is in intimate contact with the mandibular aortic arch (*m.a.*), while externally the two muscles of the hyoid arch—*i.e.*, depressor mandibulæ (*m.d.m.*) and depressor ossis hyoidei (*m.d.h.*)—approach it very closely. The proximal portion of the anterior part of the fold can be seen in the figure as a relatively broad diverticulum from the wall of the outer, inferior angle of the pharynx (*Hym.*).

Anterior to the region just considered this cord-like extension of the fold extends forward a short distance and then bends sharply outward in front of the two muscles just mentioned (fig. 18, *Hym.*, right side). In this region it enlarges considerably and finally terminates as a blind, bulbous swelling in the mesenchyme a short distance below the external epithelium. This part is shown in fig. 10 (*Tym.*), also in fig. 17 (*Tym.*).

Perhaps a clearer conception of the state of the fold may be gained by a comparison with some coronal sections. In fig. 16 we

have such a section, in which, however, the plane is lower on the right side than on the left. Commencing below, we observe on the right of the figure a short, blunt diverticulum of the pharyngeal wall, extending outward and slightly forward between the *Anlagen* of the mandibular and hyoid cartilages. This part corresponds to broad proximal portion of the fold shown in fig. 11 as continuous with the pharyngeal wall. In the fourth section dorsal to this (fig. 17) the same portion of the fold is still seen, and just external to its distal extremity is an elongated strand of like nature (*Tym.*), somewhat swollen in its outer portion, where it terminates just beneath the external epithelium. This part is the swollen portion of the cleft, which, as already mentioned, extends out in front of the hyoidean muscles and forms the distal expanded portion of the cord-like extension of the fold. In the second section above this (fig. 18) these two parts of the fold join, so that it now appears continuous throughout (*Hym.*). The present section gives a very good view of the course taken by the hyomandibular fold. One will observe that it has a very broad origin from the pharyngeal wall, and that from this point it extends outward and also considerably forward. In its middle portion the fold is considerably constricted, while in its distal outer extremity it is enlarged to form the swollen, bulbous portion which curves outward in front of the hyoidean muscles, as is well shown in the figure.

One notices that in fig. 18 the outer, distal extremity of the fold is farther removed from the exterior than in fig. 17. If the left side of fig. 16 (*Hym.*)—which represents a plane slightly more dorsal than that of the right of fig. 18—be now consulted it will be seen that this portion is still farther removed from the exterior, and by comparing the same fold (*Hym.*) in the following two figures (17 and 18) the distance between the two will be seen to be still more increased. In the latter two figures the fold approaches very closely the proximal portion of the second visceral-cleft (*2 v.f.*)—a feature to which we have already called attention.

Bringing together the facts so far obtained relating to the third stage, we shall now endeavor to form a conception of the hyomandibular fold as a whole. It arises as a solid fold of the wall of the pharynx and extends downward and obliquely forward as a thin plate between the first and second visceral-arches. Its origin from the pharynx extends downward and forward, beginning above

just anterior to the dorsal origin of the second visceral-cleft (figs. 14, 17, 18, *Hym.*) and terminating at the position of the future quadrato-mandibular articulation (fig. 10, *Hym.*). The outer or distal border begins dorsally in continuity with the roof of the pharynx (fig. 14, *Hym.*), and then extends in a gentle curve downward, outward and forward until it reaches the point where the distal, cord-like extension is given off and which I shall now designate as the "diverticulum." The latter is at first a flattened cord (fig. 11, *Eu.*), which at first extends forward a short distance, but, when it reaches the anterior border of the depressor ossis hyoidei, turns sharply outward and slightly downward in front of the latter and then expands to form a solid, bulbous swelling, which terminates blindly in the mesenchyme a short distance below the external ectoderm (figs. 10, 17, *Tym.*; also fig. 18, *Hym.*). This portion of the hyomandibular fold is the only part which comes into close proximity with the external epithelium. The remainder of the fold lies at a considerably deeper level. The distal border of the latter, below the origin of the "diverticulum," bends downward and inward and at its ventral end blends with the floor of the pharynx (figs. 10, 11, *Hym.*; 12, 13, 14, *Hym.* [left side]; 16, 17 [right]). This portion of the distal border is continuous with the ventral border of the "diverticulum," and, owing to the slightly downward direction taken by the latter, forms with it a shallow sinus or depression, the concavity of which faces downward and outward. By its anterior surface the hyomandibular fold is in close contact with the quadrate, although partly separated from it by the mandibular aortic arch (*m.a.*). Owing to the obliquely anterior direction taken by the hyomandibular fold, this surface faces both forward and upward, so that in transverse sections it appears as the dorsal border. Hence it follows that all structures found above the fold are anterior to it, whereas those ventral to it are posterior. The posterior surface faces backward and downward and has in close relation the *Anlagen* of the hyoid cartilage and associated muscles. Between the two muscles is the ramus hyomandibularis of the facial nerve (*vii h.*) which occupies its definitive position posterior to the hyomandibular fold.[9]

[9] The reader will do well to consult figure 3 of Dr. Spemann's paper, which shows a reconstruction of the hyomandibular fold of *Rana temporaria* at a similar stage. I find that the fold in *Bufo lentiginosus* is in all essential respects similar.

It now remains for us to point out the differences between the hyomandibular fold in the present and preceding stages and, if possible, to ascertain how such differences have been produced. In the first place, one will recall that the outer border of the fold in the last stage described a gentle curve, arching from above downward and forward, and that throughout the greater part of its length this border approached very closely the external epiblast. In the present stage the arch described by the outer border is interrupted about its middle by a club-shaped "diverticulum," which, again, is the only portion of the fold which approaches closely the external epithelium. The remainder of the outer border lies a considerable distance below the skin. Again, a comparison of coronal sections shows that the anterior extension of the fold is more marked than in the earlier stage. Hence there are at least three differences to be accounted for, *i.e.*, (1) the recession of the outer border of the fold from the external epithelium; (2) the formation of the blind, distal "diverticulum," which still retains the original position of the fold near the skin, and (3) the more anterior direction taken by the fold.

In order to account for these changes it is evident that at least two factors must be borne in mind. These are (1) the growth process—*i.e.*, the general increase in size of the parts in accordance with the growth of the individual—and (2) the differentiation of new structures. First, as regards the recession of the outer border of the fold from the skin: By comparing the figures illustrating the two stages, one will observe that a considerable increase in the transverse diameter of the head has taken place, whereas little, if any, increase has occurred in the vertical plane. On the other hand the pharynx has not increased concomitantly in size, but, instead, has undergone an actual decrease, so that it is not only relatively, but also absolutely, smaller in size than in the earlier stage. However, between the points of origin of the hyomandibular fold the pharyngeal cavity retains approximately its original width, a feature due to the fact that in this region it forms a pair of shallow evaginations (fig. 16). The smaller size of the pharyngeal cavity can be readily made out in the transverse sections (compare figs. 5–7 with 10–14). This reduction is in all probability connected with the increase in amount of mesenchyme and particularly with the segregation of the latter to form the *Anla-*

gen of the cartilages and muscles. The cartilages are laid down close to the wall of the pharynx, and with their increase in size the latter is naturally reduced; while at the same time the increase in amount of the general mesenchyme accounts for the increase in width of the entire head.

As a consequence of the retarded growth of the pharynx and of the increase in width of the head it follows that, unless there is sufficient rapidity of growth in the fold to compensate for the arrested growth of the pharynx, the distal extremity of the hyomandibular fold will be removed more and more from the exterior and that ultimately it will come to lie quite deeply. To such causes, I think, must be attributed the recession of the hyomandibular fold from the exterior. The head has increased in width, while the pharynx has remained stationary, and even been reduced in size, so that its appendage, the fold, quite naturally recedes from the ectoderm.

But this explanation suggests another problem: Why does the fold not exhibit sufficient rapidity of growth to enable it to retain throughout its original position near the external epithelium, as in the case of the remaining visceral-clefts, and, moreover, why does it retain this position at one point, *i.e.*, where the blind, bulbous "diverticulum" terminates? This question brings us to our second topic—the formation of the "diverticulum." This part is not, I consider, a new formation, but merely that portion of the fold which has managed by its normal growth to retain its original position near the ectoderm. In this connection I wish again to call attention to the condition in stage II. The distal border then formed a gentle arch, which for a considerable part of its extent was in close proximity to the skin. However, at both its dorsal and ventral extremities this border recedes progressively more and more from the exterior until finally it blends at both ends with the lining of the pharynx. Hence in sections the dorsal and ventral portions of the distal border are seen at varying levels below the ectoderm, while the crown (of the arched plate) is situated near the latter (compare figs. 2–7). Fig. 6 is instructive in this connection. Take the fold as shown on the right side. It will be seen that the distal edge is in close proximity to the ectoderm for a considerable part of its length. However, the upper portion of this border is closer to the ectoderm than the remainder. This

part represents a region slightly dorsal to the middle portion of the distal border. Below this the edge recedes to a slight extent from the exterior and in its middle portion forms a slight, barely perceptible depression. If we now conceive that in the future growth of the animal all the lower portion of the distal edge remains stationary and that the middle depression deepens considerably, while the upper portion alone remains in proximity to the ectoderm, then we should obtain a condition very similar to that shown in fig. 12, except that complete outward extension of the fold is not shown in the figure (see instead fig. 10). In fig. 12 the arrested ventral portion can be seen as an extension of the right inferior angle of the pharynx, while the concavity between it and the plate-like hyomandibular fold is the much-deepened depression (see also fig. 11). In the latter figure the lower portion of the fold can be seen as a blunt extension from the ventro-lateral wall of the pharynx, while the flattened, oval mass external to and above it is the dorsal portion, or, as we have temporarily termed it, the "diverticulum." More posteriorly, as shown in fig. 12, this "diverticulum" becomes continuous with the proximal portion of the fold, and accordingly the area embraced between these two portions anteriorly represents the depression, which we saw beginning in fig. 6. One will notice that in this area a muscle—the depressor mandibulæ (*m.d.m.*)—has just attained attachment to the *Anlage* of the quadrate cartilage, while external to it its companion muscle, the depressor ossis hyoidei (*m.d.h.*), has acquired attachment to the tip of the processus muscularis. The "diverticulum" lies between these two muscles and, as already mentioned, extends anteriorly between them until it reaches the anterior surface of the outer muscle (depressor ossis hyoidei), around which it curves outward (fig. 10, also 17 and 18). In the behavior of these two muscles lies the clue to the solution of the problem under consideration. One will recall that both of these muscles belong originally to the hyoid arch, and consequently their acquirement of attachment to the quadrate is a later affair. In stage II the original hyoidean muscle-mass, from which these two are subsequently differentiated, extends in its long axis almost vertically and is situated entirely behind the hyomandibular fold (see figs. 2–7). Later, however, as the muscle increases in size its long axis becomes extended in an obliquely anterior direction,

the superior border facing forward. At this time the common muscle divides into an inner and anterior mass, the depressor mandibulæ, and an outer and posterior mass, the depressor ossis hyoidei. With subsequent growth both muscles extend forward more and more until one of them—the depressor mandibulæ—invades the area intervening between the skin and the inferior portion of the distal edge of the hyomandibular fold at the point indicated by the slight depression shown in fig. 6 (x). Here its anterior extremity comes into close relation with the segregating *Anlage* of the quadrate at a point just in front of and below the fold. The outer muscle—the depressor ossis hyoidei—also acquires attachment to the quadrate *Anlage*, but at a point above and posterior to the fold.

I have just mentioned that the depressor mandibulæ extends forward in the space between the lower portion of the distal border of the hyomandibular fold and the skin. With this invasion an effective barrier is interposed between the two; and as a result of the subsequent increase in size of the muscle and of the extension in width of the head, it follows that this lower portion of the hyomandibular fold will be arrested in its growth and will consequently come to be more and more removed from the exterior. At the same time the segregation of the mesenchyme to form cartilage *Anlagen* interposes additional barriers to the outward growth of the fold. Hence it is possible to understand why it is that the lower part of the fold should lie so far beneath the ectoderm as shown in the present stage (figs. 11, 16, 17). On the other hand, the dorsal portion of the hyomandibular fold—*i.e.*, that which forms the "diverticulum"—is situated above the depressor mandibulæ, so that the latter does not interfere with its normal growth and as a result this portion of the fold still retains its proximity to the skin. With the increase in width of the head it has been carried outward with the skin. In its proximal portion, however, this part also has been encroached upon by the developing depressor mandibulæ, and as a result it presents the form of a long-drawn-out cord, narrow and flattened in its proximal part and swollen in its terminal part, where it is not encroached upon to any great extent by the surrounding structures.

Along the dorsal edge of the fold no well-marked changes, so far as I have been able to determine, seem to have taken place.

In the figures (particularly figs. 17 and 18 [left side]) one will notice that the distal extremity is removed some distance from the skin, but this appearance, I consider, is simply produced by the obliquely ventral direction taken by the dorsal border, as has been already described.

This brings us to our third problem, *i.e.*, the more pronounced anterior extension of the fold. This, I consider, is correlated with the growth anteriorly of the two hyoidean muscles. Naturally as these extend forward they carry the fold with them. As a result of this the posterior surface of the fold comes to face outward, and the anterior inward. Hence in transverse sections structures external to the fold are also morphologically posterior, whilst those internal to it are morphologically anterior (compare transverse with coronal sections of present stage).

Stage IV.—Young tadpole. Opercular fold well developed, ending freely posteriorly and with the ends of the external gills protruding beyond its posterior margin. The various tissues for the most part clearly differentiated. True cartilage developed in the mandibular and hyoid arches (Pl. VIII, figs. 15, 19; Pl. IX, figs. 23, 24).

Beginning anteriorly the distal, blind extremity of the "diverticulum" appears as a transversely extended cord of cells, somewhat expanded distally, lying in the loose mesenchyme some distance below the external epithelium (fig. 24, *Tym.*). This cord is clearly distinguished from the surrounding fibrous tissue by its greater density, which naturally causes it to stain more deeply, and also by the presence within its substance of yolk spherules and numerous pigment granules, similar to those found in the mucous membrane of the pharynx. In the present stage the yolk spherules, although still present, are much less numerous than in the earlier stages and they soon disappear altogether, so that the dark pigment becomes the distinguishing feature of the cord. The lower proximal portion of the hyomandibular fold can be seen in the figure as a shallow protrusion (*Hym.*) from the ventro-lateral angle of the pharynx (compare with figs. 10 and 11). In the region immediately posterior the proximal portion is practically blended with the wall of the pharynx (figs. 15 and 19). In fig. 19 (right side) it again becomes distinguishable and soon becomes continuous with the prominent diverticulum *Eu.* (left side of fig. 19).

I will now return to the "diverticulum" in order to trace its further course. From its distal extremity the "diverticulum" extends inward and slightly backward in close contact with the anterior surface of the depressor ossis hyoidei (*m.d.h.*, fig. 24, *Tym.*), and then ascending slightly to pass over a large vessel, the mandibular aortic arch (*m.a.*), it comes into close relation with the external surface of the processus muscularis of the quadrate. As it progresses inward the cord gradually decreases in diameter, so that when it reaches the quadrate it is reduced to about a half or even a third of the diameter of its distal expanded portion.

After reaching the external surface of the quadrate the reduced "diverticulum" turns sharply posteriorly at the inner edge of the depressor ossis hyoidei as a minute, cylindrical cord, (figs. 23, 15, 19, *Eu.*). Here it is closely applied to the processus muscularis of the quadrate. Below and internal to it is the mandibular aortic arch (*m. a.*), while bounding it externally is a small, accessory slip from the depressor mandibulæ (fig. 15, *m.d.m'.*), the main body of which is attached to the quadrate anterior and internal to the cord (fig. 24, *m.d.m.*). The cord extends posteriorly in the same position, usually closely applied to the quadrate, and showing more or less reduction in size, so that in certain parts of its course it is difficult to trace clearly. Throughout its entire extent, however, it contains numerous pigment granules, the presence of which facilitates considerably the tracing of the cord, as does also the scattered yolk-bodies apparent for the last time in the present stage.

In fig. 15 the cord can be seen, much reduced, just under the transversely extended processus muscularis and external to the mandibular aortic arch (*m.a.*). In fig. 19 (right side) the cord (*Eu.*) still occupies the same relative position. Just external to it is the ramus hyomandibularis of the facial nerve (*vii h.*). Internal to it the mandibular artery (*m.a.*) intervenes between it and the pharyngeal wall. At this point the mandibular aortic arch begins to turn inward in order to reach the carotid. Immediately behind the artery the cord fuses with the distal extremity of the diverticulum extending up from the pharyngeal wall (see fig. 19, *Eu.*, left side). Here both the cord and proximal portion of the hyomandibular fold become continuous. The fold becomes more prominent in the following sections (fig. 23, *Eu.*) and ultimately

blends with the wall of the pharynx dorsal to the inner opening of the first branchial-cleft.

To recapitulate briefly the state of the hyomandibular fold at the present stage: we have found the ventral portion of the fold present only as an inconspicuous protrusion of the ventro-lateral angle of the pharynx. Only the dorsalmost portion of the original fold is well developed, and from this the greatly prolonged "diverticulum" extends forward as a solid cord of cells. The latter originates posterior to the quadrato-hyoid articulation. Throughout the greater part of its length the cord is closely applied to the outer surface of the processus muscularis. Anteriorly, however, it bends sharply outward in front of the depressor ossis hyoidei and terminates blindly as a somewhat bulbous enlargement in the subcutaneous tissue.

I may here describe briefly the condition of the neighboring skeletal structures, since in the present stage these have acquired the relations which they retain throughout the entire larval period. The animal has now passed beyond the pro-cartilage stage and consequently the cartilages can be readily traced. In most cases they already show a well-defined perichondrium. The quadrate cartilage is prolonged in an antero-posterior direction almost parallel with the corresponding trabecula cranii. Its course is thus quite the reverse of that which characterizes its adult condition. Its distal articular end is prolonged as the processus articularis downward and forward to a point beneath the anterior surface of the eye and at a later period still farther forward. At its distal extremity it bears the transversely placed mandibular cartilage (Meckel's). The greater part of the quadrate is prolonged upward and outward as a stout plate immediately underlying the orbit—the processus muscularis—to the outer side of which are attached the depressor mandibulæ and depressor ossis hyoidei. In the concavity formed in the inner (and upper) surface are lodged the muscles of mastication (fig. 24, *k.m.*). On the ventral surface near the point of junction between the body of the cartilage and the processus muscularis there is forming at the present stage a shallow, concave articular surface for the head of the hyoid cartilage. The latter is a stout bar of cartilage extending transversely beneath the floor of the pharynx and joined to its fellow of the opposite side by the intervention of a median plate, the

copula. In its outer portion the hyoid turns sharply upward to form an ascending process, which articulates with the quadrate.

In its anterior portion—*i.e.*, where the processus articularis is given off—the quadrate is joined to the trabecula of the same side by an ascending bar of cartilage, the commissura quadrato-cranialis anterior (Gaupp) or palato-pterygoid bar. Posteriorly again the quadrate bends sharply upward and then as a stout bar (processus ascendens, fig. 19, *Pr.A.*) extends inward back of the eye and in front of the auditory capsule to join with the trabecula just in front of the basilar plate (parachordal). There is no distinct separation between these connected cartilages, the matrix of each being perfectly continuous with that of the others.

It now remains to connect the conditions observed in the present stage with those seen in the preceding. The chief differences between the former and the latter are briefly these: (1) The relatively much greater length of the "diverticulum," a condition associated with the removal of the part connecting it with the pharyngeal wall to a point more posterior, *i.e.*, back of the quadrato-hyoid articulation; (2) the reduction in size of the middle portion of the "diverticulum," and (3) the almost complete obliteration of the ventro-anterior portion of the hyomandibular fold.

These differences are, I believe, correlated with a continuation of the same processes treated of under the description of the preceding stage. These are chiefly the modifications undergone by the neighboring muscles and cartilages. The general growth of the animal has had little, if anything, to do in producing the differences between the two stages. There has been a considerable increase in width of the head—an increase in which, however, the contained structures have taken part. The greater length of the "diverticulum" has been produced by the continued increase in depth of the depression in the distal border of the fold. In stage III this depression was relatively shallow, so that the "diverticulum" was very short and blunt. In the present stage the "diverticulum" is very long, having the form of a long, narrow cord somewhat expanded at its distal extremity. The insinking of the distal border was associated with the growth of the depressor mandibulæ, in consequence of the latter's acquisition of a point of attachment to the quadrate in front of and below the distal border of the hyomandibular fold. In the present stage this muscle has

increased in size and extended its area of attachment to the quadrate. It has also given off an accessory slip, which extends upward external to the cord-like "diverticulum" to attach to the processus muscularis (fig. 15, *m.d.m'.*). Moreover, immediately behind the posterior edge of the depressor mandibulæ, the hyoid cartilage is drawn up to form an articulation with the quadrate, and following this the enlarged mandibular aortic arch turns inward to join with the carotid (fig. 19, *m.a.*) just in front of the point where the "diverticulum" joins the extension from the pharyngeal wall (fig. 19, *Eu.*, left side). Thus changes in three structures have been instrumental in producing the deepening of the depression, *i.e.*, (1) the increase in size and area of attachment of the depressor mandibulæ; (2) the articulation of the hyoid to the quadrate, and (3) the increase in size of the mandibular aortic arch.

The reduction in size of the middle portion of the "diverticular" cord (compare figures with fig. 11 of last stage) has been associated with two factors: (1) the increase in size of the accompanying mandibular aorta, and (2) the differentiation and growth of the outer, accessory slip of the depressor mandibulæ. By examining figure 15, one will notice the reduced cord tightly wedged in between the enlarged artery internally and the accessory slip externally.

The decrease of the ventro-anterior portion of the hyomandibular fold to form a mere shallow protrusion of the ventro-lateral angle of the pharynx (fig. 24, *Hym.*) has in all probability been produced by the deepening of the depression and its final blending with the pharyngeal wall. Naturally, as the depression deepened its deepest part would ultimately blend with the pharyngeal wall, so as to be no longer distinguishable (fig. 15). As the ventro-anterior portion of the fold formed the lower border of the depression, it would naturally be drawn in with the deepening of the depression until it formed the shallow protrusion mentioned (fig. 24, *Hym.*). This decrease is also accelerated by the increase in size and density of the skeletal and muscular parts.

Stage V.—Young tadpole of about 9 mm. Opercular cavity communicating with the exterior by a single opening on the left side. No external gills.

The condition of the hyomandibular fold is essentially similar to

that in the preceding stage. The tissues of the animal are more compact and definitely limited than in the last stage. The external, distal extremity of the "diverticulum" (or, as I may now term it, the Eustachian cord, since the structure under consideration ultimately gives rise to the greater part of the tube of that name) has the same general appearance as before. It, however, does not extend so far out from the processus muscularis as before, a condition probably produced by the increase in size of the process. A slight reduction has also taken part in this portion of the cord ("diverticulum"). More marked, however, has been the change in the middle portion of the cord. After extending inward to the processus muscularis the cord rapidly degenerates, becoming greatly flattened and much reduced in size, so that for a part of its course it is very difficult to recognize, the presence of scattered nuclei and numerous pigment granules alone serving to mark its existence. This great reduction has been associated with a continuation of the processes described in the last stage, *i.e.*, the growth of the hyoidean muscles (depressor mandibulæ and depressor ossis hyoidei), the articulation of the hyoid with the quadrate and the increase in size of the mandibular artery (Pl. VII, fig. 8 and Pl. IX, fig. 25, *Eu.*).

The cord retains the degenerate condition just described until it reaches a point just back of the region where the mandibular aorta turns inward to join the carotid. A good idea of the condition of the cord can be obtained from coronal sections (fig. 8). In such it appears as a faint, narrow cord (*Eu.*), coursing in an antero-posterior direction in contact with the outer surface of the processus muscularis. This cord contains no lumen and shows no indication of a tubal character. It contains throughout its course scattered nuclei arranged end to end, and it is largely colored by numerous black pigment-granules. The yolk-spherules have now disappeared entirely. There is very little substance to the cord and in places where nuclei and pigment are lacking it becomes very difficult to trace.

Immediately posterior to the inflexed mandibular aorta the Eustachian cord is joined to the pharyngeal wall by a narrow strand of somewhat elongated cells. These cells are not easily distinguishable from the cells of the surrounding connective tissue, but they form a rather dense patch in the latter stretched between

the pharyngeal wall and the tubal *Anlage*. Immediately beyond this region this connecting portion broadens out considerably to form a rather shallow bulging of cells from the roof of a "lateral recess" (fig. 25, *l.r.*) or pouch of the pharynx, from the outer extremity of which the thymus gland is given off. This "lateral recess" is really formed by an extension outward of the branchial portion of the pharynx over the internal branchial openings, so that the latter are now situated on the floor of the cavity. In the preceding stage this "lateral recess" was just beginning to form as a slight bulging beneath the proximal portion of the tubal *Anlage*. With the extension externally of the "lateral recess" the proximal portion of the Eustachian cord comes to appear as an inconspicuous protuberance over the inner part of the roof of the "recess" (fig. 25, immediately internal to *vii h*).

Stage VI.—Tadpole of 18 mm. Posterior limbs appearing as minute buds below the root of the tail (Pl. IX, fig. 26).

In this stage the Eustachian cord has about reached the height of its degeneration. The cord still maintains the same general relations to the surrounding parts as before. Its distal, expanded extremity remains distinct, and from thence the cord can readily be traced to its characteristic position next to the outer surface of the processus muscularis. Here, however, it soon becomes very small and then can be traced only with the greatest difficulty. The cord lies immediately above the mandibular aorta, and by following the latter it may be traced as a minute, more or less flattened pigmented patch, which in certain parts contains one or two nuclei not readily distinguishable from the nuclei of the surrounding fibrous tissue (fig. 26, *Eu.*). Immediately posterior to the quadrato-hyoid articulation the cord again enlarges slightly and can be traced thence for a considerable distance. Then in the region where the ramus hyomandibularis begins to come into close relations with its external surface all distinct traces of the cord are lost. Nothing more of the cord is to be made out until we come to the region where the mandibular artery turns inward, where for a short space the cord is again revealed and then terminates without forming any clear connection with the pharyngeal wall. This most posterior fragment of the cord is situated below the quadrate, dorsal to the upper anterior end of the "lateral recess" of the pharynx. There is no distinct proliferation from the dorso-

internal wall of this portion to indicate the proximal, connecting part of the tubal cord. The proliferation has very likely opened out with the formation of the "lateral recess," and has been merged into the dorsal wall of the latter.

It thus appears that in the present stage the Eustachian cord for the greater part of its length has undergone remarkable fragmentation, having broken up into a number of sections of variable length. Each of these fragments, however, retains exactly the same relations to the surrounding structures that the corresponding part of the cord showed in the preceding stage. It is quite possible that the various fragments may still be connected by the transparent cell-walls of the cord, and in that case the apparent fragmentation is simply due to the restriction of the more vital, stainable portions to areas less subject to the action of unfavorable forces. I am somewhat inclined to consider this the actual condition in the present stage, since in a longitudinal series I have been enabled to follow out with great care a pale, almost transparent cord connecting some of the fragments. Posteriorly this cord approaches very closely the wall of the pharynx. I have not been able to make out any distinct connection between the two, but their proximity would incline me to believe such a union to exist. Still I have not been able to satisfy myself on this point.

I have not been able to determine to my satisfaction the factors which have been concerned in the degeneration of the Eustachian cord. One of them is probably to be found in the pressure exerted by the surrounding structures, particularly by the two muscles already mentioned. Owing probably to its unfavorable position the tubal cord appears to have little, if any, power of independent growth. It therefore may have been acted on by the growth anteriorly of the head whereby a pull has been exerted on it, causing its wall to extend and its contents to be restricted to more or less limited regions of the cord.

Stage VII.—Tadpole of 21 mm. Hind limbs well developed.

This stage very closely resembles the preceding. Owing to an accident the more anterior sections of the Eustachian cord in the specimen examined are lacking, but I have no doubt but that this portion of the cord in the present stage corresponds in all essential respects with that in the preceding, since in the succeeding stage the anterior portion is very similar to that in stage VI. So far

as the remaining parts are concerned, they present the same fragmentary character as in the preceding stage, being in certain locations almost unrecognizable. I noticed in the present series (and likewise in several later ones) that there is no necessary correspondence either in the number, length or distribution of the fragments of the two sides. In the case of the specimen of the present stage examined the sections were almost exactly transverse, so that the same parts were cut on both sides. Yet the tubal cord may be present for a considerable distance on one side and apparently altogether absent on the other. This irregularity is a marked feature during the entire metamorphic period. I find that there is also marked individual variation in this respect. This variability would seem to indicate that the character of the fragmentation is not due to some inherited tendency, but is produced by mechanical forces exerted by the surrounding structures.

Posteriorly the Eustachian cord terminates suddenly in the usual position, dorsal to the anterior extremity of the "lateral recess" of the branchial portion of the pharynx. In the same region a prominent proliferation arises from the dorsal wall of the "recess," and extends upward to the same relative position as that occupied by the cord in the more anterior sections. This structure may represent the same mass of cells which originally established the connection between the tubal cord and the wall of the pharynx, but of this interpretation I am uncertain, since I was unable to discover any sign of such proliferation in the preceding stage or in a number of later stages. Possibly its occurrence or absence is a matter of individual variation.

There has been but little change in the skeleton since the last period. Posteriorly, however, the quadrate has developed a posteriorly projecting processus oticus, which comes in contact with the ventral surface of the auditory capsule. The processus oticus arises at the angle formed by the body of the quadrate with the processus ascendens. The stapes appears for the first time as an oval chondrification within the membrane closing the fenestra ovalis. There are no distinct traces of a columella auris.

Stage VIII.—Tadpole of 21 mm. Preceding the appearance of the fore-limbs.

At this time we have the earliest distinct appearance of the annular cartilage (Pl. IX, fig. 28, *An.*). About opposite the point where

the pterygo-palatine bar (processus quadrato-cranialis anterior) joins the quadrate, a very conspicuous proliferation from the perichondrium of the latter occurs. This proliferation forms a dense strand of cells, which reach outward in the subcutaneous tissue and aggregate themselves in a somewhat concentric fashion about the distal, expanded termination of the Eustachian cord (*Tym.*). The dense patch there formed is the *Anlage* of the future annular cartilage. From this region the Eustachian cord pursues the same course that characterized the preceding stages. The cord is, however, much more distinct than in any of the latter, and its tubular character is plainly indicated by its nuclei, which are now grouped about the periphery of the cord, thus giving the latter the appearance of a duct with an obliterated lumen (Pl. XI, fig. 29, *Eu.*). In certain parts of the cord slight indications of a central lumen can be made out, but, as a rule, any cavities that do appear are neither very extensive nor pronounced. The cord, however, as in the preceding stages, becomes smaller as it extends posteriorly and in the region of the quadrato-hyoid articulation disappears. It soon reappears, however. Posterior to the hyoid articulation the cord again becomes much reduced, but does not lose its continuity with the most posterior portion. In the most posterior part of its course the cord again enlarges, becomes clearly tubular, and exhibits a more or less well-defined lumen. In this portion the cord occupies its characteristic position, ventral to the quadrate cartilage and internal to the ramus hyomandibularis, which in the region of the quadrato-hyoid articulation ascends from the ventral portion of the hyoid arch to come into close relation with the outer wall of the cord. From the dorsal wall of the "lateral recess" of the pharynx a conspicuous strand of cells arises, the dorsal end of which closely approaches the Eustachian cord, but before actual contact takes place the cord rather suddenly terminates. I am not certain of the significance of this strand. It may be the part which originally connected the cord with the pharynx, but of this I am uncertain, since I found no evidence of it in stage VI.

Stage IX.—Tadpole of 18 mm. Both fore and hind limbs present.

This stage marks the commencement of the metamorphosis. Since the changes which the Eustachian cord (or tube) undergoes during this period are obviously correlated with modifications

blends with the wall of the pharynx dorsal to the inner opening of the first branchial-cleft.

To recapitulate briefly the state of the hyomandibular fold at the present stage: we have found the ventral portion of the fold present only as an inconspicuous protrusion of the ventro-lateral angle of the pharynx. Only the dorsalmost portion of the original fold is well developed, and from this the greatly prolonged "diverticulum" extends forward as a solid cord of cells. The latter originates posterior to the quadrato-hyoid articulation. Throughout the greater part of its length the cord is closely applied to the outer surface of the processus muscularis. Anteriorly, however, it bends sharply outward in front of the depressor ossis hyoidei and terminates blindly as a somewhat bulbous enlargement in the subcutaneous tissue.

I may here describe briefly the condition of the neighboring skeletal structures, since in the present stage these have acquired the relations which they retain throughout the entire larval period. The animal has now passed beyond the pro-cartilage stage and consequently the cartilages can be readily traced. In most cases they already show a well-defined perichondrium. The quadrate cartilage is prolonged in an antero-posterior direction almost parallel with the corresponding trabecula cranii. Its course is thus quite the reverse of that which characterizes its adult condition. Its distal articular end is prolonged as the processus articularis downward and forward to a point beneath the anterior surface of the eye and at a later period still farther forward. At its distal extremity it bears the transversely placed mandibular cartilage (Meckel's). The greater part of the quadrate is prolonged upward and outward as a stout plate immediately underlying the orbit—the processus muscularis—to the outer side of which are attached the depressor mandibulæ and depressor ossis hyoidei. In the concavity formed in the inner (and upper) surface are lodged the muscles of mastication (fig. 24, *k.m.*). On the ventral surface near the point of junction between the body of the cartilage and the processus muscularis there is forming at the present stage a shallow, concave articular surface for the head of the hyoid cartilage. The latter is a stout bar of cartilage extending transversely beneath the floor of the pharynx and joined to its fellow of the opposite side by the intervention of a median plate, the

copula. In its outer portion the hyoid turns sharply upward to form an ascending process, which articulates with the quadrate.

In its anterior portion—*i.e.*, where the processus articularis is given off—the quadrate is joined to the trabecula of the same side by an ascending bar of cartilage, the commissura quadrato-cranialis anterior (Gaupp) or palato-pterygoid bar. Posteriorly again the quadrate bends sharply upward and then as a stout bar (processus ascendens, fig. 19, *Pr.A.*) extends inward back of the eye and in front of the auditory capsule to join with the trabecula just in front of the basilar plate (parachordal). There is no distinct separation between these connected cartilages, the matrix of each being perfectly continuous with that of the others.

It now remains to connect the conditions observed in the present stage with those seen in the preceding. The chief differences between the former and the latter are briefly these: (1) The relatively much greater length of the "diverticulum," a condition associated with the removal of the part connecting it with the pharyngeal wall to a point more posterior, *i.e.*, back of the quadrato-hyoid articulation; (2) the reduction in size of the middle portion of the "diverticulum," and (3) the almost complete obliteration of the ventro-anterior portion of the hyomandibular fold.

These differences are, I believe, correlated with a continuation of the same processes treated of under the description of the preceding stage. These are chiefly the modifications undergone by the neighboring muscles and cartilages. The general growth of the animal has had little, if anything, to do in producing the differences between the two stages. There has been a considerable increase in width of the head—an increase in which, however, the contained structures have taken part. The greater length of the "diverticulum" has been produced by the continued increase in depth of the depression in the distal border of the fold. In stage III this depression was relatively shallow, so that the "diverticulum" was very short and blunt. In the present stage the "diverticulum" is very long, having the form of a long, narrow cord somewhat expanded at its distal extremity. The insinking of the distal border was associated with the growth of the depressor mandibulæ, in consequence of the latter's acquisition of a point of attachment to the quadrate in front of and below the distal border of the hyomandibular fold. In the present stage this muscle has

blends with the wall of the pharynx dorsal to the inner opening of the first branchial-cleft.

To recapitulate briefly the state of the hyomandibular fold at the present stage: we have found the ventral portion of the fold present only as an inconspicuous protrusion of the ventro-lateral angle of the pharynx. Only the dorsalmost portion of the original fold is well developed, and from this the greatly prolonged "diverticulum" extends forward as a solid cord of cells. The latter originates posterior to the quadrato-hyoid articulation. Throughout the greater part of its length the cord is closely applied to the outer surface of the processus muscularis. Anteriorly, however, it bends sharply outward in front of the depressor ossis hyoidei and terminates blindly as a somewhat bulbous enlargement in the subcutaneous tissue.

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copula. In its outer portion the hyoid turns sharply upward to form an ascending process, which articulates with the quadrate.

In its anterior portion—*i.e.*, where the processus articularis is given off—the quadrate is joined to the trabecula of the same side by an ascending bar of cartilage, the commissura quadrato-cranialis anterior (Gaupp) or palato-pterygoid bar. Posteriorly again the quadrate bends sharply upward and then as a stout bar (processus ascendens, fig. 19, *Pr.A.*) extends inward back of the eye and in front of the auditory capsule to join with the trabecula just in front of the basilar plate (parachordal). There is no distinct separation between these connected cartilages, the matrix of each being perfectly continuous with that of the others.

It now remains to connect the conditions observed in the present stage with those seen in the preceding. The chief differences between the former and the latter are briefly these: (1) The relatively much greater length of the "diverticulum," a condition associated with the removal of the part connecting it with the pharyngeal wall to a point more posterior, *i.e.*, back of the quadrato-hyoid articulation; (2) the reduction in size of the middle portion of the "diverticulum," and (3) the almost complete obliteration of the ventro-anterior portion of the hyomandibular fold.

These differences are, I believe, correlated with a continuation of the same processes treated of under the description of the preceding stage. These are chiefly the modifications undergone by the neighboring muscles and cartilages. The general growth of the animal has had little, if anything, to do in producing the differences between the two stages. There has been a considerable increase in width of the head—an increase in which, however, the contained structures have taken part. The greater length of the "diverticulum" has been produced by the continued increase in depth of the depression in the distal border of the fold. In stage III this depression was relatively shallow, so that the "diverticulum" was very short and blunt. In the present stage the "diverticulum" is very long, having the form of a long, narrow cord somewhat expanded at its distal extremity. The insinking of the distal border was associated with the growth of the depressor mandibulæ, in consequence of the latter's acquisition of a point of attachment to the quadrate in front of and below the distal border of the hyomandibular fold. In the present stage this muscle has

increased in size and extended its area of attachment to the quadrate. It has also given off an accessory slip, which extends upward external to the cord-like "diverticulum" to attach to the processus muscularis (fig. 15, *m.d.m'.*). Moreover, immediately behind the posterior edge of the depressor mandibulæ, the hyoid cartilage is drawn up to form an articulation with the quadrate, and following this the enlarged mandibular aortic arch turns inward to join with the carotid (fig. 19, *m.a.*) just in front of the point where the "diverticulum" joins the extension from the pharyngeal wall (fig. 19, *Eu.*, left side). Thus changes in three structures have been instrumental in producing the deepening of the depression, *i.e.*, (1) the increase in size and area of attachment of the depressor mandibulæ; (2) the articulation of the hyoid to the quadrate, and (3) the increase in size of the mandibular aortic arch.

The reduction in size of the middle portion of the "diverticular" cord (compare figures with fig. 11 of last stage) has been associated with two factors: (1) the increase in size of the accompanying mandibular aorta, and (2) the differentiation and growth of the outer, accessory slip of the depressor mandibulæ. By examining figure 15, one will notice the reduced cord tightly wedged in between the enlarged artery internally and the accessory slip externally.

The decrease of the ventro-anterior portion of the hyomandibular fold to form a mere shallow protrusion of the ventro-lateral angle of the pharynx (fig. 24, *Hym.*) has in all probability been produced by the deepening of the depression and its final blending with the pharyngeal wall. Naturally, as the depression deepened its deepest part would ultimately blend with the pharyngeal wall, so as to be no longer distinguishable (fig. 15). As the ventro-anterior portion of the fold formed the lower border of the depression, it would naturally be drawn in with the deepening of the depression until it formed the shallow protrusion mentioned (fig. 24, *Hym.*). This decrease is also accelerated by the increase in size and density of the skeletal and muscular parts.

Stage V.—Young tadpole of about 9 mm. Opercular cavity communicating with the exterior by a single opening on the left side. No external gills.

The condition of the hyomandibular fold is essentially similar to

that in the preceding stage. The tissues of the animal are more compact and definitely limited than in the last stage. The external, distal extremity of the "diverticulum" (or, as I may now term it, the Eustachian cord, since the structure under consideration ultimately gives rise to the greater part of the tube of that name) has the same general appearance as before. It, however, does not extend so far out from the processus muscularis as before, a condition probably produced by the increase in size of the process. A slight reduction has also taken part in this portion of the cord ("diverticulum"). More marked, however, has been the change in the middle portion of the cord. After extending inward to the processus muscularis the cord rapidly degenerates, becoming greatly flattened and much reduced in size, so that for a part of its course it is very difficult to recognize, the presence of scattered nuclei and numerous pigment granules alone serving to mark its existence. This great reduction has been associated with a continuation of the processes described in the last stage, *i.e.*, the growth of the hyoidean muscles (depressor mandibulæ and depressor ossis hyoidei), the articulation of the hyoid with the quadrate and the increase in size of the mandibular artery (Pl. VII, fig. 8 and Pl. IX, fig. 25, *Eu.*).

The cord retains the degenerate condition just described until it reaches a point just back of the region where the mandibular aorta turns inward to join the carotid. A good idea of the condition of the cord can be obtained from coronal sections (fig. 8). In such it appears as a faint, narrow cord (*Eu.*), coursing in an antero-posterior direction in contact with the outer surface of the processus muscularis. This cord contains no lumen and shows no indication of a tubal character. It contains throughout its course scattered nuclei arranged end to end, and it is largely colored by numerous black pigment-granules. The yolk-spherules have now disappeared entirely. There is very little substance to the cord and in places where nuclei and pigment are lacking it becomes very difficult to trace.

Immediately posterior to the inflexed mandibular aorta the Eustachian cord is joined to the pharyngeal wall by a narrow strand of somewhat elongated cells. These cells are not easily distinguishable from the cells of the surrounding connective tissue, but they form a rather dense patch in the latter stretched between

the pharyngeal wall and the tubal *Anlage.* Immediately beyond this region this connecting portion broadens out considerably to form a rather shallow bulging of cells from the roof of a "lateral recess" (fig. 25, *l.r.*) or pouch of the pharynx, from the outer extremity of which the thymus gland is given off. This "lateral recess" is really formed by an extension outward of the branchial portion of the pharynx over the internal branchial openings, so that the latter are now situated on the floor of the cavity. In the preceding stage this "lateral recess" was just beginning to form as a slight bulging beneath the proximal portion of the tubal *Anlage.* With the extension externally of the "lateral recess" the proximal portion of the Eustachian cord comes to appear as an inconspicuous protuberance over the inner part of the roof of the "recess" (fig. 25, immediately internal to *vii h*).

Stage VI.—Tadpole of 18 mm. Posterior limbs appearing as minute buds below the root of the tail (Pl. IX, fig. 26).

In this stage the Eustachian cord has about reached the height of its degeneration. The cord still maintains the same general relations to the surrounding parts as before. Its distal, expanded extremity remains distinct, and from thence the cord can readily be traced to its characteristic position next to the outer surface of the processus muscularis. Here, however, it soon becomes very small and then can be traced only with the greatest difficulty. The cord lies immediately above the mandibular aorta, and by following the latter it may be traced as a minute, more or less flattened pigmented patch, which in certain parts contains one or two nuclei not readily distinguishable from the nuclei of the surrounding fibrous tissue (fig. 26, *Eu.*). Immediately posterior to the quadrato-hyoid articulation the cord again enlarges slightly and can be traced thence for a considerable distance. Then in the region where the ramus hyomandibularis begins to come into close relations with its external surface all distinct traces of the cord are lost. Nothing more of the cord is to be made out until we come to the region where the mandibular artery turns inward, where for a short space the cord is again revealed and then terminates without forming any clear connection with the pharyngeal wall. This most posterior fragment of the cord is situated below the quadrate, dorsal to the upper anterior end of the "lateral recess" of the pharynx. There is no distinct proliferation from the dorso-

internal wall of this portion to indicate the proximal, connecting part of the tubal cord. The proliferation has very likely opened out with the formation of the "lateral recess," and has been merged into the dorsal wall of the latter.

It thus appears that in the present stage the Eustachian cord for the greater part of its length has undergone remarkable fragmentation, having broken up into a number of sections of variable length. Each of these fragments, however, retains exactly the same relations to the surrounding structures that the corresponding part of the cord showed in the preceding stage. It is quite possible that the various fragments may still be connected by the transparent cell-walls of the cord, and in that case the apparent fragmentation is simply due to the restriction of the more vital, stainable portions to areas less subject to the action of unfavorable forces. I am somewhat inclined to consider this the actual condition in the present stage, since in a longitudinal series I have been enabled to follow out with great care a pale, almost transparent cord connecting some of the fragments. Posteriorly this cord approaches very closely the wall of the pharynx. I have not been able to make out any distinct connection between the two, but their proximity would incline me to believe such a union to exist. Still I have not been able to satisfy myself on this point.

I have not been able to determine to my satisfaction the factors which have been concerned in the degeneration of the Eustachian cord. One of them is probably to be found in the pressure exerted by the surrounding structures, particularly by the two muscles already mentioned. Owing probably to its unfavorable position the tubal cord appears to have little, if any, power of independent growth. It therefore may have been acted on by the growth anteriorly of the head whereby a pull has been exerted on it, causing its wall to extend and its contents to be restricted to more or less limited regions of the cord.

Stage VII.—Tadpole of 21 mm. Hind limbs well developed.

This stage very closely resembles the preceding. Owing to an accident the more anterior sections of the Eustachian cord in the specimen examined are lacking, but I have no doubt but that this portion of the cord in the present stage corresponds in all essential respects with that in the preceding, since in the succeeding stage the anterior portion is very similar to that in stage VI. So far

as the remaining parts are concerned, they present the same fragmentary character as in the preceding stage, being in certain locations almost unrecognizable. I noticed in the present series (and likewise in several later ones) that there is no necessary correspondence either in the number, length or distribution of the fragments of the two sides. In the case of the specimen of the present stage examined the sections were almost exactly transverse, so that the same parts were cut on both sides. Yet the tubal cord may be present for a considerable distance on one side and apparently altogether absent on the other. This irregularity is a marked feature during the entire metamorphic period. I find that there is also marked individual variation in this respect. This variability would seem to indicate that the character of the fragmentation is not due to some inherited tendency, but is produced by mechanical forces exerted by the surrounding structures.

Posteriorly the Eustachian cord terminates suddenly in the usual position, dorsal to the anterior extremity of the "lateral recess" of the branchial portion of the pharynx. In the same region a prominent proliferation arises from the dorsal wall of the "recess," and extends upward to the same relative position as that occupied by the cord in the more anterior sections. This structure may represent the same mass of cells which originally established the connection between the tubal cord and the wall of the pharynx, but of this interpretation I am uncertain, since I was unable to discover any sign of such proliferation in the preceding stage or in a number of later stages. Possibly its occurrence or absence is a matter of individual variation.

There has been but little change in the skeleton since the last period. Posteriorly, however, the quadrate has developed a posteriorly projecting processus oticus, which comes in contact with the ventral surface of the auditory capsule. The processus oticus arises at the angle formed by the body of the quadrate with the processus ascendens. The stapes appears for the first time as an oval chondrification within the membrane closing the fenestra ovalis. There are no distinct traces of a columella auris.

Stage VIII.—Tadpole of 21 mm. Preceding the appearance of the fore-limbs.

At this time we have the earliest distinct appearance of the annular cartilage (Pl. IX, fig. 28, *An.*). About opposite the point where

the pterygo-palatine bar (processus quadrato-cranialis anterior) joins the quadrate, a very conspicuous proliferation from the perichondrium of the latter occurs. This proliferation forms a dense strand of cells, which reach outward in the subcutaneous tissue and aggregate themselves in a somewhat concentric fashion about the distal, expanded termination of the Eustachian cord (*Tym.*). The dense patch there formed is the *Anlage* of the future annular cartilage. From this region the Eustachian cord pursues the same course that characterized the preceding stages. The cord is, however, much more distinct than in any of the latter, and its tubular character is plainly indicated by its nuclei, which are now grouped about the periphery of the cord, thus giving the latter the appearance of a duct with an obliterated lumen (Pl. XI, fig. 29, *Eu.*). In certain parts of the cord slight indications of a central lumen can be made out, but, as a rule, any cavities that do appear are neither very extensive nor pronounced. The cord, however, as in the preceding stages, becomes smaller as it extends posteriorly and in the region of the quadrato-hyoid articulation disappears. It soon reappears, however. Posterior to the hyoid articulation the cord again becomes much reduced, but does not lose its continuity with the most posterior portion. In the most posterior part of its course the cord again enlarges, becomes clearly tubular, and exhibits a more or less well-defined lumen. In this portion the cord occupies its characteristic position, ventral to the quadrate cartilage and internal to the ramus hyomandibularis, which in the region of the quadrato-hyoid articulation ascends from the ventral portion of the hyoid arch to come into close relation with the outer wall of the cord. From the dorsal wall of the "lateral recess" of the pharynx a conspicuous strand of cells arises, the dorsal end of which closely approaches the Eustachian cord, but before actual contact takes place the cord rather suddenly terminates. I am not certain of the significance of this strand. It may be the part which originally connected the cord with the pharynx, but of this I am uncertain, since I found no evidence of it in stage VI.

Stage IX.—Tadpole of 18 mm. Both fore and hind limbs present.

This stage marks the commencement of the metamorphosis. Since the changes which the Eustachian cord (or tube) undergoes during this period are obviously correlated with modifications

taking place simultaneously in the skeletal structures, it is necessary, in order to follow the former, to obtain a right conception of the latter. Hence in the present stage I will first treat of the essential skeletal parts. In the first place, the axis of the quadrate extends in a more dorso-ventral direction than formerly, so that now the mandibular articulation lies below the anterior edge of the eye, instead of being entirely in front of it as before. This position implies that the lower part of the quadrate has moved or rotated backward through a slight angle. The processus quadrato-cranialis anterior (pterygo-palatine) is now considerably elongated in an antero-posterior direction, a change obviously associated with the backward rotation of the quadrate. The processus muscularis (orbital) begins to show signs of degeneration, especially along its dorso-external edge. The hyoid still articulates to the ventral surface of the quadrate. Posteriorly the processus ascendens has degenerated and consequently the quadrate has lost its connection with the wall of the brain-case, but instead it now joins by means of its processus oticus the wall of the auditory capsule anterior to the fenestra ovalis. In the membrane closing the latter the stapes now appears as a large, oval mass of fully differentiated cartilage. The columella auris is a delicate rod of primitive cartilage, closely applied to the wall of the capsule. Anteriorly it terminates without forming any connection whatever with either the quadrate or any portion of the Eustachian tube and posteriorly it unites with the stapes. The columella is most distinct and its tissue most compact in its posterior portion, so that it cannot be regarded as a derivative of the quadrate.

As a consequence of the posterior rotation of the distal portion of the quadrate, the distal extremity of the Eustachian cord is now situated somewhat posterior to its former position, but its relation to the immediately surrounding structures is the same as before, since these likewise have been affected by the quadrate's change of axis. The annular cartilage, now a dense cellular mass, is situated under the anterior margin of the eye and above the mandibular articulation. To its ventral surface the more anterior fibres of the depressor ossis hyoidei have acquired attachment. Imbedded in the cartilage is the distal end of the Eustachian cord, the future tympanic cavity. The general appearance of the cord is similar to that in the preceding stage. The cord still shows

fragmentation, although the length and distribution of the fragments differ on the two sides. No connection between the cord and the pharynx can be determined with certainty, although the proliferation attached to the dorsal wall of the "lateral recess" is still present.

Stage X.—Tailed toad of 15.5 mm. Fore and hind limbs well developed.

This stage very closely resembles the preceding, the most marked differences being the greater antero-posterior elongation of the processus quadrato-cranialis anterior and the associated greater posterior rotation of the quadrate. The Eustachian cord, also, is very distinct, particularly in its anterior and posterior portions. In the region just back of the quadrato-hyoid articulation it is greatly reduced and traceable only with difficulty. In several places the cord shows a distinct lumen. There are no distinct signs of a proliferation attached to the pharyngeal wall extending toward the cord.

Stage XI.—Tailed toad, 6.8 mm., tail 1.5 mm. Close of the metamorphosis.

The processus quadrato-cranialis anterior has now increased considerably in length, so that it extends in a direct antero-posterior direction as in the adult toad. The axis of the quadrate has attained an almost vertical direction, but it still extends somewhat forward, its distal, articular end being located under the middle or posterior part of the eye. The hyoid still maintains its union with the quadrate. More posteriorly, in the region of the auditory capsule, the columella auris can be traced farther forward. At its anterior, distal extremity it is prolonged forward as a dense strand of cells, which forms a connection with the posterior surface of the quadrate. Only the more posterior portion of the columellar rod is formed of true cartilage, the anterior portion being as yet only a dense, undifferentiated mass of cells.

The most conspicuous changes which the tympano-Eustachian tube has undergone since the preceding period have been associated with the change of axis of the suspensory cartilages. As a result of this the tympanic portion of the tube, together with the annular cartilage, has moved backward to a region below the posterior portion of the eye. The tube, as a whole, exhibits the same fragmentary character as hitherto, and I have remarked here,

as in a number of other stages, a difference in the condition of the tubes of the two sides. Posteriorly the tube terminates without forming any connection with the pharynx. The proliferation from the pharynx is not very distinct. It probably tends to disappear in connection with the degeneration of the branchial apparatus.

Stage XII.—Tailed toad, 7 mm. Close of metamorphosis.

The quadrate cartilage now stands almost vertical, its distal, articular extremity lying under the posterior border of the eye. The hyoid bar has separated completely from the quadrate and its dorsal extremity is now joined by the intervention of a dense strand of cells to the base of the auditory capsule.

The distal part of the tympano-Eustachian tube now lies immediately posterior and ventral to the eye. Since the distal portion of the quadrate rotates backward more rapidly than the remaining part, it results that the posterior, hitherto ventral, surface of the cartilage forms a shallow concavity. From this behavior it follows that the distal, expanded portion of the tube—*i.e.*, tympanic portion—comes to lie farther posterior in relation to the rest of the cord, so that the latter no longer presents an almost direct antero-posterior course, but instead now lies in an almost transverse plane, except for a slight anterior inclination. The tympanic region of the tube is thus brought into relation with the auditory capsule. In the present period it has not quite reached the region of the latter, but is not far removed, being located just back of the eye. Another feature shown by the present stage is the union of the various fragments of which it was hitherto composed. This union is also probably to be connected with the quadrate's change of axis, since this would result in carrying the more anterior fragments backward and thus bringing them into closer relation with the posterior parts. At present the tube can be traced without a break throughout its entire course. This fact speaks strongly for the view that these parts have all along been united by an attenuated cord. The fragments are simply the contents of this cord which have been restricted to certain areas. As a result of the backward rotation of the quadrate, the stretching to which the cord had hitherto been subjected is relieved and accordingly the various fragments of the substance flow together, thus producing the union described. Proximally, however, the tube forms no con-

nection with the pharyngeal wall, but immediately internal to its proximal termination the pharynx sends out a narrow cleft between the hyoid and the base of the auditory capsule. Posteriorly the tube ceases immediately in front of the dense strand connecting the hyoid cornua with the auditory capsule, so that at this stage the tube occupies its definitive position between the quadrate and hyoid cartilages. As a result of the changes that have taken place in the hyoid its nerve, the ramus hyomandibularis, now lies ventral and posterior to the tube—a position which characterizes it in the adult condition. In the branchial region the entire branchial apparatus, including the "lateral recess" of the pharynx, has become largely obliterated.

Stage XIII.—Young toad, 6 mm. Metamorphosis complete.

This period marks the close of the metamorphosis. The inferior, articular portion of the quadrate extends more posterior, so that the quadrate on its posterior surface shows a marked concavity. The general course of the quadrate is about as follows: Dorsally from its union with the base of the auditory capsule it extends forward and downward for some little distance, it then describes a wide curve downward and backward for the remainder of its length, so that its distal end, bearing the mandibular cartilage, now comes to lie under or even slightly behind its dorsal, proximal extremity. The hyoid arch is now fused completely with the auditory capsule, the intervening cellular strand having become cartilaginous.

The annular cartilage is now located posterior to the eye and ventral to the anterior portion of the auditory capsule. It closely underlies the skin and is external to the outer surface of the quadrate. The Eustachian tube itself differs but little from its condition in the preceding stage, except that its lumen, where present, is more distinct and extensive. A short distance above the tube the distal extremity of the columella auris may be observed as a dense cellular mass, which posteriorly grades into true cartilage.

Stage XIV.—Young toad, about 9 mm (figs. 30, 31).

In this stage the tympano-Eustachian passage has the same general position and relations that distinguish it in the fully mature animal. Relatively it is not so large as in the latter, nor is its lumen complete throughout, but in all other respects it is essentially

like the adult structure. Figs. 30 and 31 illustrate the condition of the tube at this time. In fig. 30 we have a transverse section through one side of the head immediately back of the eye. To the outer side is shown the quadrate cartilage, which in the present stage stands almost vertical and hence is shown in the figure cut throughout the greater part of its length. External to the upper portion of the cartilage is the tympanic portion of the Eustachian tube, showing a slight lumen (*Tym.*). I have another specimen of approximately the same age in which the lumen is much larger, forming a considerable cavity. Underlying this portion is the tympanic or annular cartilage, which in its ventral portion, at least, is completely chondrified (*An.*). The fully formed cartilage does not, however, form a complete ring. Internally the tube approaches the outer surface of the quadrate, as was the case in the earlier stages. Applied to the dorso-external wall of the tympanic cavity is the distal extremity of the columella auris, at present a very compact cellular mass, not yet differentiated into true cartilage (*Cl.*). The apparent inclusion of the columella within the tympanic cavity is produced by the subsequent growth of the latter around this portion of the cartilage. Attached to the ventral surface of the annular cartilage are fibres of the depressor ossis hyoidei (*m.d.h.*). The attachment of the muscle to the cartilage was acquired soon after the earliest *Anlage* of the latter had appeared. At its ventral end the muscle has lost its attachment to the hyoid cartilage and has acquired a new insertion into the angle of the mandible, so that like the depressor mandibulæ it serves to depress the latter (compare also fig. 31). The bulk of the muscle lies posterior to the Eustachian tube. Internal to the muscle and between it and the quadrate are two blood-vessels, which correspond to the original mandibular aorta (*m.a.*). This vessel, as we have seen, was an important one during the tadpole period, but during the metamorphosis it underwent some profound changes. Its middle portion largely degenerated, so that the vessel became divided into a proximal and a distal half. The vessel undergoes other changes, but these I have not been able to follow satisfactorily with the material at hand.

Fig. 31 shows a section through the tympano-Eustachian tube near its posterior boundary. The quadrate (*q.*) is here seen in two separate portions, a dorsal and a ventral. This condition can

be readily understood by referring to the description of the cartilage as given in stage XIII. It suffices to mention that the section passes back of the point where the quadrate curves backward on itself, so that the dorsal is the proximal, the ventral the distal portion of the cartilage. The distal portion bears the mandible. Underlying the proximal portion is the Eustachian tube (*Eu.*), here shown in three detached segments. Other sections, however, show these segments continuous, so that the tube is now complete. Moreover, the proximal innermost segment is continuous with the pharynx and in reality represents a diverticulum (*div.*) from the latter. In the other specimen that I have of this stage this portion is continuous with the pharynx, but its distal extremity ends blindly without forming a connection with the Eustachian tube. In the toad of stage XIII this diverticulum of the pharynx was also present, and connecting it with the widely separated tubal *Anlage* was a dense strand of connective tissue cells, whose long diameters were extended in a direction coinciding with a line drawn between the separated parts. By means of this diverticulum the tympano-Eustachian tube is now united to the pharynx. The tube presents throughout an irregular lumen, bounded by a well-defined columnar epithelium. That portion of the tube which is most externally situated is the posterior part of the tympanic cavity (*Tym.*). Attached to the dorsal wall of the latter is the columella auris (*Cl.*). The ramus hyomandibularis of the facial nerve is not shown in this section, since, owing to the posterior flexure of the quadrate and the separation of the hyoid from the latter, the nerve now lies entirely posterior to the tube.

SUMMARY.

The results recorded in the preceding pages may be briefly summarized as follows:

1. The tympano-Eustachian passage is in the main derived from the dorsalmost portion of the hyomandibular fold (cleft).

2. In the earliest stages described, the hyomandibular fold is present as a solid, plate-like fold extending outward and forward beneath the eye region and terminating laterally in a free edge situated a short distance below the ectoderm. Its attachment to the ectoderm is lost at about this stage.

3. At first the outer or distal edge of the hyomandibular fold is smooth and unbroken throughout its entire extent. Later, this edge becomes interrupted in its middle portion by the formation of a progressively deepening depression, which ultimately reaches the pharyngeal wall and divides the hyomandibular fold into two parts—a dorsal cord-like portion, the future tympano-Eustachian passage, and a ventral portion forming a shallow sacculation to the ventro-lateral portion of the pharyngeal cavity.

4. The ventral portion of the hyomandibular fold ceases to be recognizable after the late tadpole stages. It is this portion which Villy considers as the last remnant of the hyomandibular fold.

5. The earliest evidence of the degeneration of the hyomandibular fold is afforded by the recession of its outer edge from the neighborhood of the external ectoderm. Only the dorsalmost portion of the fold continues in intimate proximity to the skin. The withdrawal of the remainder is associated with (1) the reduction in size of the pharynx, in consequence of the segregation of the surrounding mesenchyme to form the *Anlagen* of muscles and cartilages, and (2) the development of the muscles of the hyoid arch—the depressor mandibulæ and ossis hyoidei. Of these muscles the depressor mandibulæ extends forward between the skin and the outer border of the hyomandibular fold and acquires attachment to the developing quadrate cartilage in front of the fold. It thus interposes an effective barrier to further outward extension of the fold. Only the dorsalmost portion of the fold remains unimpeded by the muscle, and this accordingly retains its proximity to the ectoderm and in the subsequent growth of the head is carried outward as a narrow, cord-like strand expanded at its outer extremity into a club-shaped swelling. This portion I have designated the "diverticulum." It is the *Anlage* of the tympano-Eustachian passage.

6. The outer hyoidean muscle, the depressor ossis hyoidei, also acquires attachment to the quadrate *Anlage* at a point above and posterior to the hyomandibular cleft. The "diverticulum" or *Anlage* of the tympano-Eustachian passage thus comes to lie between the two hyoidean muscles.

7. The growth anteriorly of the hyoidean muscles produces a marked antero-posterior extension of the hyomandibular fold and of its derivative, the tympano-Eustachian *Anlage*. This antero-

posterior direction taken by the tubal *Anlage* is characteristic of it during the entire larval period.

8. The further degeneration of the hyomandibular fold is correlated with the subsequent increase in size of the muscles already mentioned, the union of the hyoid cartilage with the quadrate and the enlargement of the mandibular aortic arch.

9. After the degeneration of the hyomandibular fold the *Anlage* of the tympano-Eustachian passage persists as a minute, solid cord, extending along the outer surface of the processus muscularis of the quadrate. Posteriorly it is attached to the wall of the pharynx at a point posterior to the quadrato-hyoid articulation. Anteriorly and distally it expands to form the club-shaped *Anlage* of the tympanic cavity.

10. During the active tadpole period the tympano-Eustachian *Anlage* undergoes marked degeneration. This degeneration is confined to the middle and posterior parts of the *Anlage,* the distal expanded portion retaining its original relative size throughout the entire larval period. The degeneration is in all probability connected with the growth of the two muscles—depressor mandibulæ and ossis hyoidei—between which it lies. Owing to the lack of space it is unable to keep pace with the surrounding structures in the subsequent growth of the animal.

11. In the early tadpole period the tympano-Eustachian *Anlage* is continuous posteriorly with the wall of the pharynx. Later the connection between the two apparently disappears, though the time of its disappearance seems to vary in different individuals. An indistinct strand may continue to unite the two parts, but this I have been unable to demonstrate.

12. The degeneration of the tympano-Eustachian *Anlage* is carried to an extreme in the later tadpole stages. At this time it is apparently broken up into a number of fragments of varying length. This fragmentation is probably more apparent than real, being produced by the restriction of the more vital stainable substance of the tubal *Anlage* to areas less subject to the pressure of the neighboring structures. The irregular distribution of the fragments, both in different individuals and on different sides of the same individual, favors the view that a compressed, transparent cord still connects the apparently separate parts. In one specimen

(tadpole of about 18 mm.) I have been enabled to trace out such a connecting cord.

13. Regeneration of the tympano-Eustachian *Anlage* begins at a period immediately preceding the period when the fore-limbs break out of the opercular cavity.

14. The later metamorphosis of the tubal *Anlage* is connected with the modifications of the neighboring skeletal structures, particularly with the posterior rotation of the quadrate. By this means the tubal cord comes into relation with the auditory region of the skull and the various fragments are brought closer together, so that they can readily unite.

15. The acquisition of a lumen by the tubal *Anlage* takes place gradually, beginning at the close of the metamorphosis. Details apparently vary in different individuals.

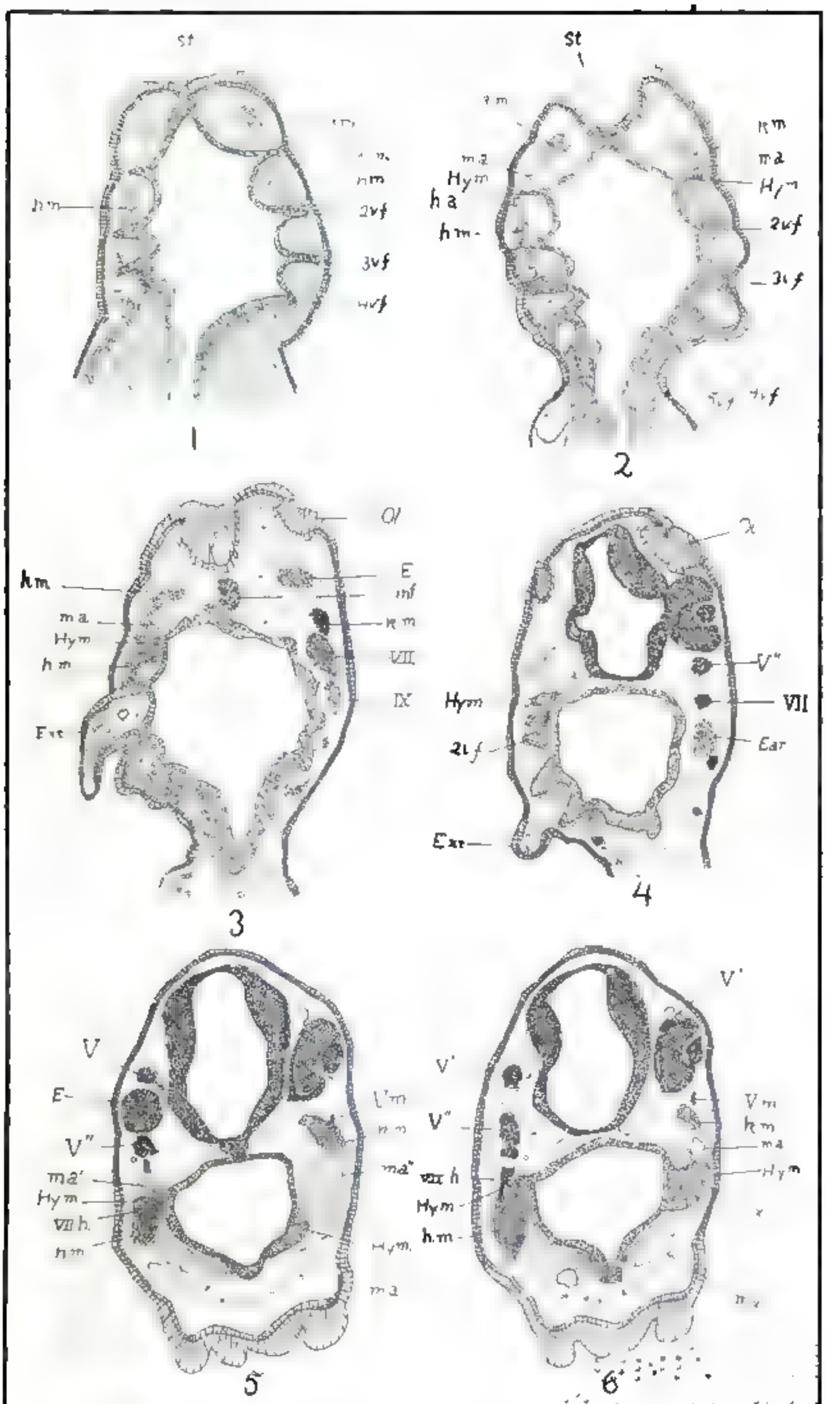
16. Completion of the tympano-Eustachian passage is effected by an outgrowth from the pharynx which unites with the tubal *Anlage.*

17. The final position of the tympano-Eustachian tube between the mandibular and hyoid bars is produced by the separation of the latter from the quadrate and its attachment to the auditory capsule posterior to the tube.

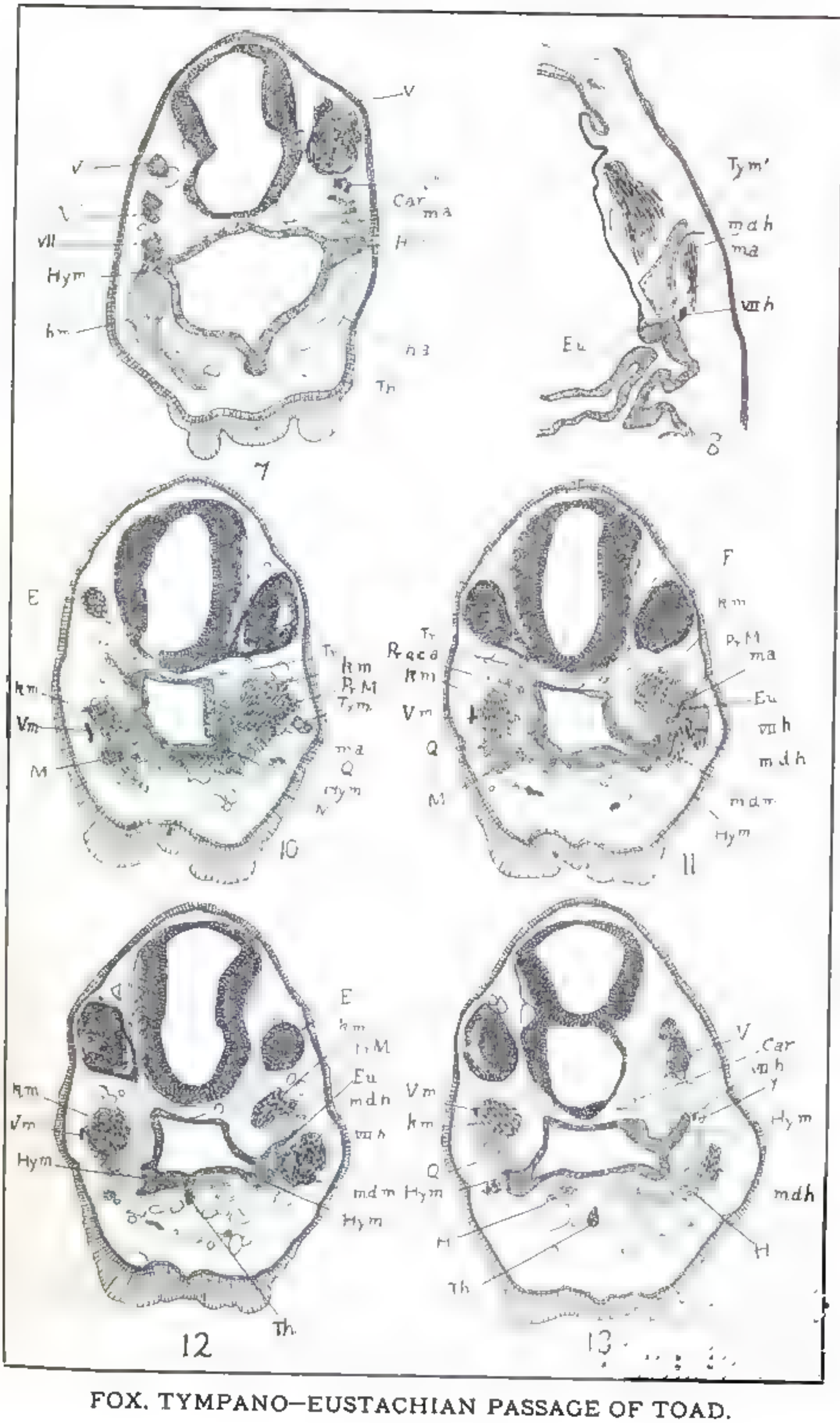
18. The annular cartilage arises at a stage immediately preceding the protrusion of the fore-limbs. Its *Anlage* forms a dense cellular strand derived from the perichondrium of the quadrate and surrounding the tympanic portion of the tubal *Anlage.* It does not begin to form fully differentiated cartilage until after the close of the metamorphosis.

19. The stapes arises within the membrane closing the fenestra ovalis. It has no connection with any of the visceral-arches.

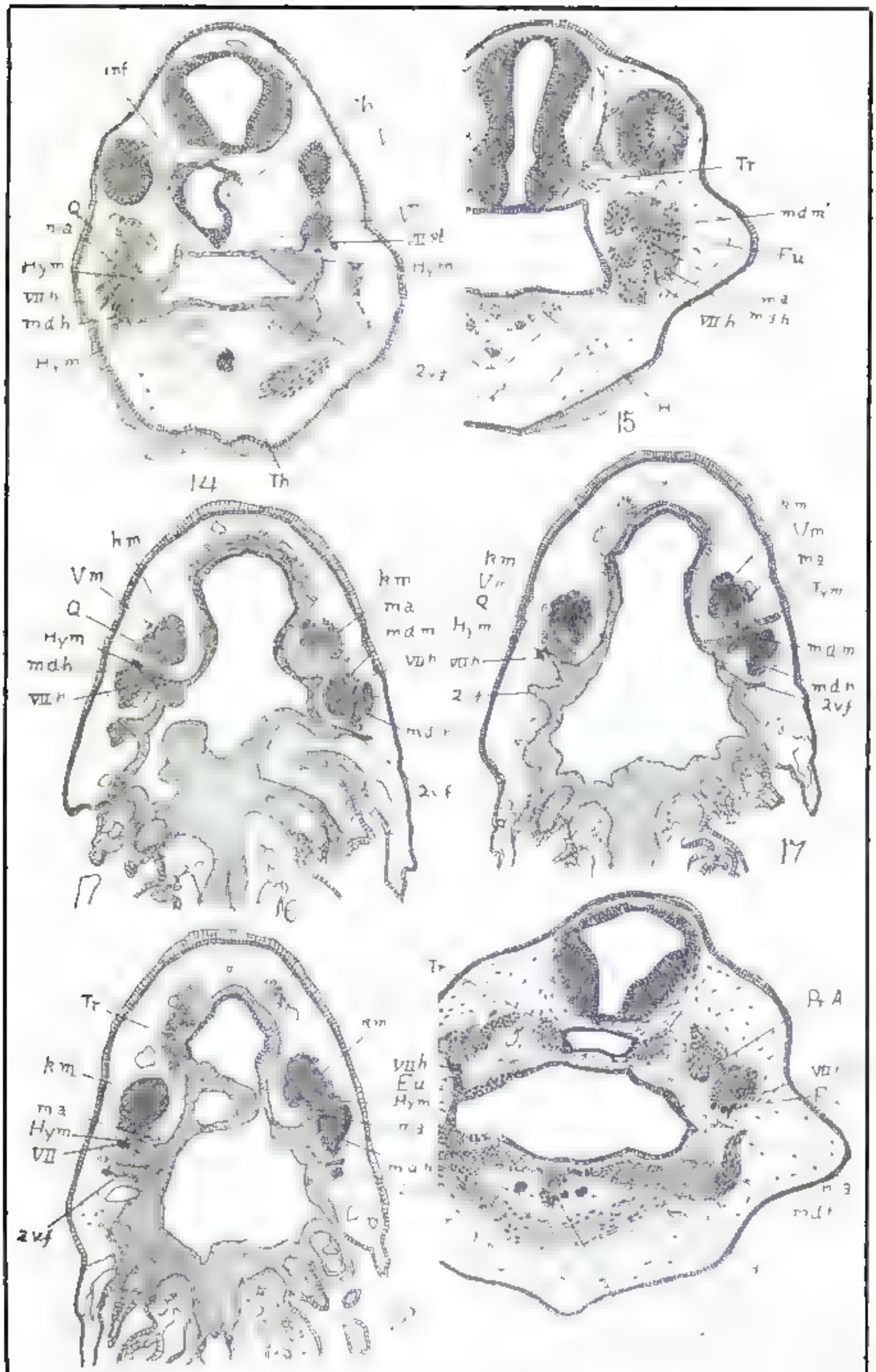
20. The columella auris is first met with in the early stages of the metamorphosis, as a compact cellular strand extending forward from the stapes and terminating imperceptibly in the connective tissue. It continues to grow forward and acquires connection with the quadrate. Continued growth brings it in contact with the tympanic cavity. Chondrification begins in the posterior portion of the rod.



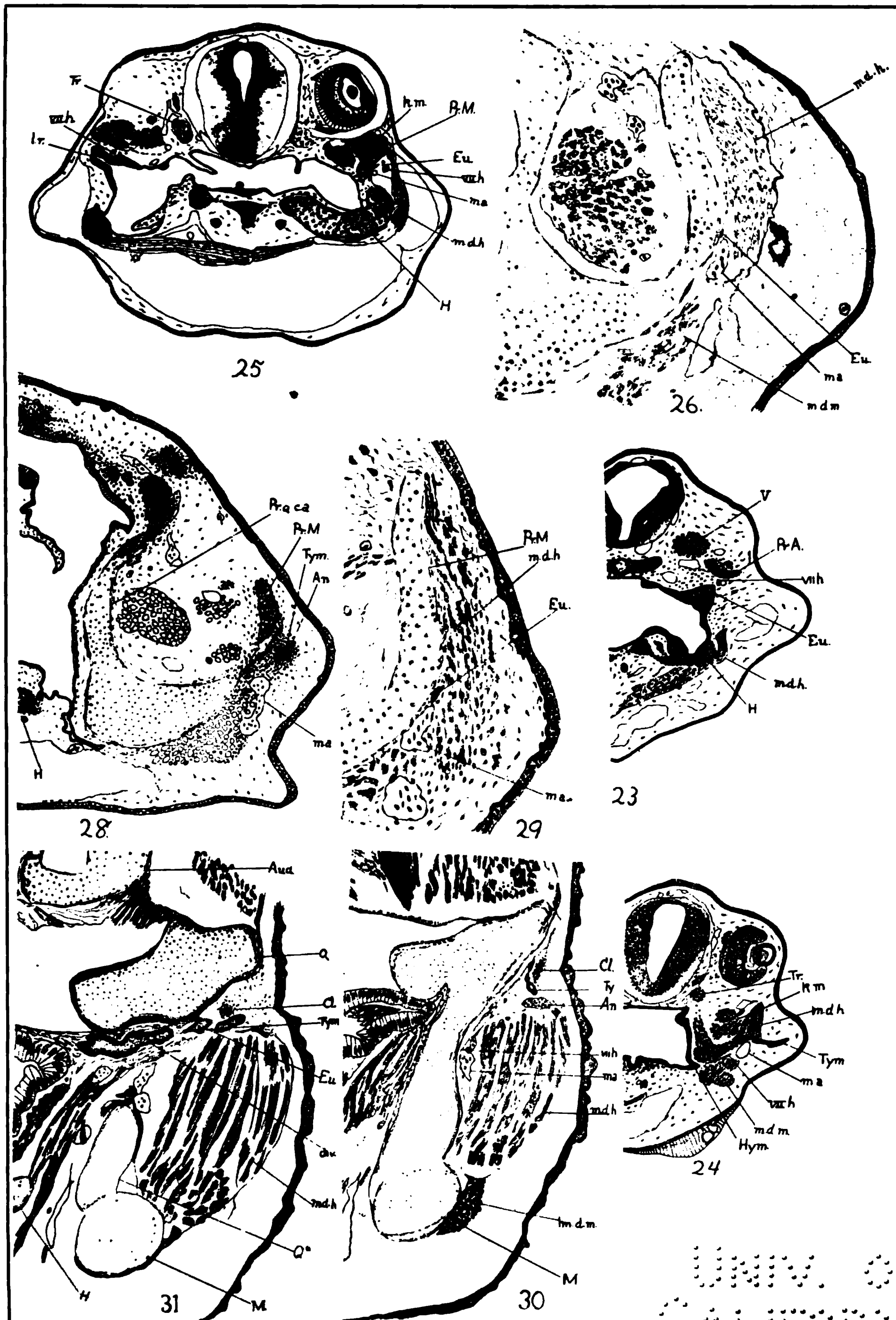
FOX. TYMPANO—EUSTACHIAN PASSAGE OF TOAD.



FOX. TYMPANO–EUSTACHIAN PASSAGE OF TOAD.



FOX. TYMPANO—EUSTACHIAN PASSAGE OF TOAD.



FOX. TYMPANO—EUSTACHIAN PASSAGE OF TOAD.

EXPLANATION OF PLATES VI, VII, VIII, IX.

The drawings were outlined by aid of the camera lucida, and with the exception of figures 26 and 29 were all drawn to the same scale. With the exception of the two mentioned they are also slightly diagramatic—those on plates VI-VIII reduced one-third; on plate IX, one-half.

REFERENCE LETTERS.

An.—Annular cartilage.
Aud.—Auditory capsule.
Car.—Carotid artery.
Ch.—Chorda.
Cl.—Columella auris.
div.—Diverticulum from pharynx.
E.—Eye.
Eu.—Eustachian cord (or tube).
Ext.—External gill.
H.—Hyoid cartilage.
h.a.—Hyoidean aortic arch.
h.m.—Hyoidean muscle mass.
Hym.—Hyomandibular fold.
inf.—Infundibulum.
k.m.—Muscles of mastication.
l.r.—Lateral recess of pharynx.
M.—Meckel's cartilage.
m.a.—Mandibular aortic arch.
m.a′.—Its efferent portion.
m.a′′.—Its afferent portion.
m.d.h.—Depressor hyoidei.
m.d.m.—Depressor mandibulæ.
m.d.m′.—Its accessory slip.
Ol.—Olfactory depression.
Pr.A.—Processus ascendens.
Pr.q.c.a. — Commissura quadrato-cranialis anterior.
Pr.M.—Processus muscularis.
Q.—Quadrate.
St.—Stomatodeal plate.
Th.—Thyroid.
Tr.—Trabecula cranii.
Tym.—Tympanic (distal) portion of Eustachian cord.
X.—Small blood-vessel connecting mandibular and hyoid aortic arches.
Y.—Small blood-vessel external to ramus hyomandibularis.
2, 3, 4, 5, v.f.—Second, third, fourth and fifth visceral-clefts.
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V′.—Ophthalmic ganglion.
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Fig. 8.—Coronal section of head of tadpole of stage V. One side alone shown.

Fig. 10.—Transverse section of the head of a young tadpole of stage III. The section is through the anterior end of the pharynx. The plane of section is more posterior on the right side than on the left.

Fig. 11.—Fourth section posterior to that of figure 10. *Eu.* designates the "diverticulum," while at *Hym.* is the antero-inferior portion of the hyomandibular fold.

Fig. 12.—Third section posterior to the last. The diverticulum (*Eu.*) is now continuous with the antero-inferior portion (*Hym.*) of the hyomandibular fold. Between the two is the depression lodging the muscles (*m.d.m.* and *m.d.h.*). The small vessel above *Eu.* is the mandibular aortic arch.

Fig. 13.—Sixth section posterior to the last. The mandibular aortic arch is dorsal to *Hym.*

Plate VIII, Fig. 14.—Third section posterior to last. The mandibular aortic arch on the right side is just internal to *vii pl.*

Fig. 15.—Transverse section of head of tadpole of stage IV in the region immediately posterior to that shown in figure 24.

Fig. 16.—Coronal section of the head of a young tadpole of stage II. On the right side the section passes a slight distance above the floor of the pharynx, while on the left it is considerably higher. The small vessel in front of *Hym.* is the mandibular aortic arch.

Fig. 17.—Fourth section dorsal to the last. On the right side the little protrusion of the pharyngeal wall just internal to *Tym.* is the antero-inferior portion of the hyomandibular fold just below the point where it becomes continuous with *Tym.* The space between the two is the depression.

Fig. 18.—Coronal section of the head of the same animal a slight distance below the roof of the mouth.

Fig. 19.—Transverse section of the head of a tadpole of stage IV in the region of the processus ascendens.

Plate IX, Fig. 23.—Transverse section of the head of a tadpole of stage IV, passing through a region slightly anterior to the auditory sac.

Fig. 24.—Transverse section of the head of a tadpole of stage IV, showing the anterior expanded portion (*Tym.*) of the Eustachian cord. *Hym.* denotes the proximal anterior portion of the hyomandibular cleft.

Fig. 25.—Transverse section of the head of a tadpole of stage V. On the left the section is immediately posterior to the eye. The minute upgrowth from the dorsal wall of *l.r.* just internal to *vii h.* is the Eustachian proliferation.

Fig. 26.—Transverse section of a portion of the right side of the head of an old tadpole of 18 mm. (stage VI). This section is considerably more magnified than the others and is intended to show the extremely rudimentary character of the Eustachian cord at this stage.

Fig. 28.—Transverse section of the right side of the head of a tadpole at the beginning of the metamorphosis (stage VIII), showing the formation of the annular cartilage.

Fig. 29.—Transverse section of a portion of the right side of the head of the same animal. The section was drawn with the same degree of magnification as figure 26 and is intended to show the Eustachian cord when it begins to regenerate.

Fig. 30.—Transverse section through one side of the head of a young toad (stage XV). The section passes through the region immediately in front of the ear-capsule.

Fig. 31.—Transverse section through one side of the head of the same animal. The section passes through the anterior portion of the ear-capsule.

Haughton

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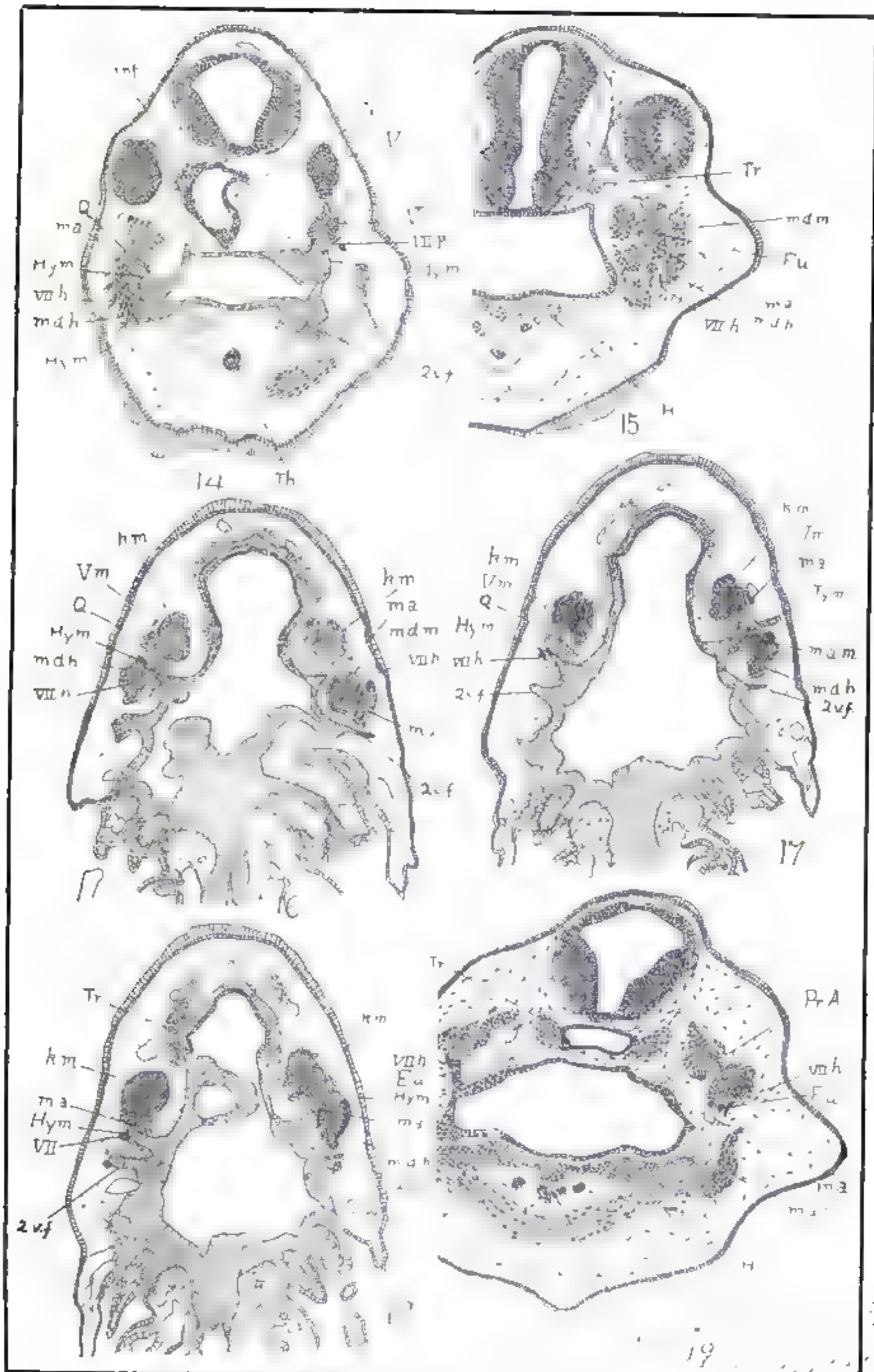

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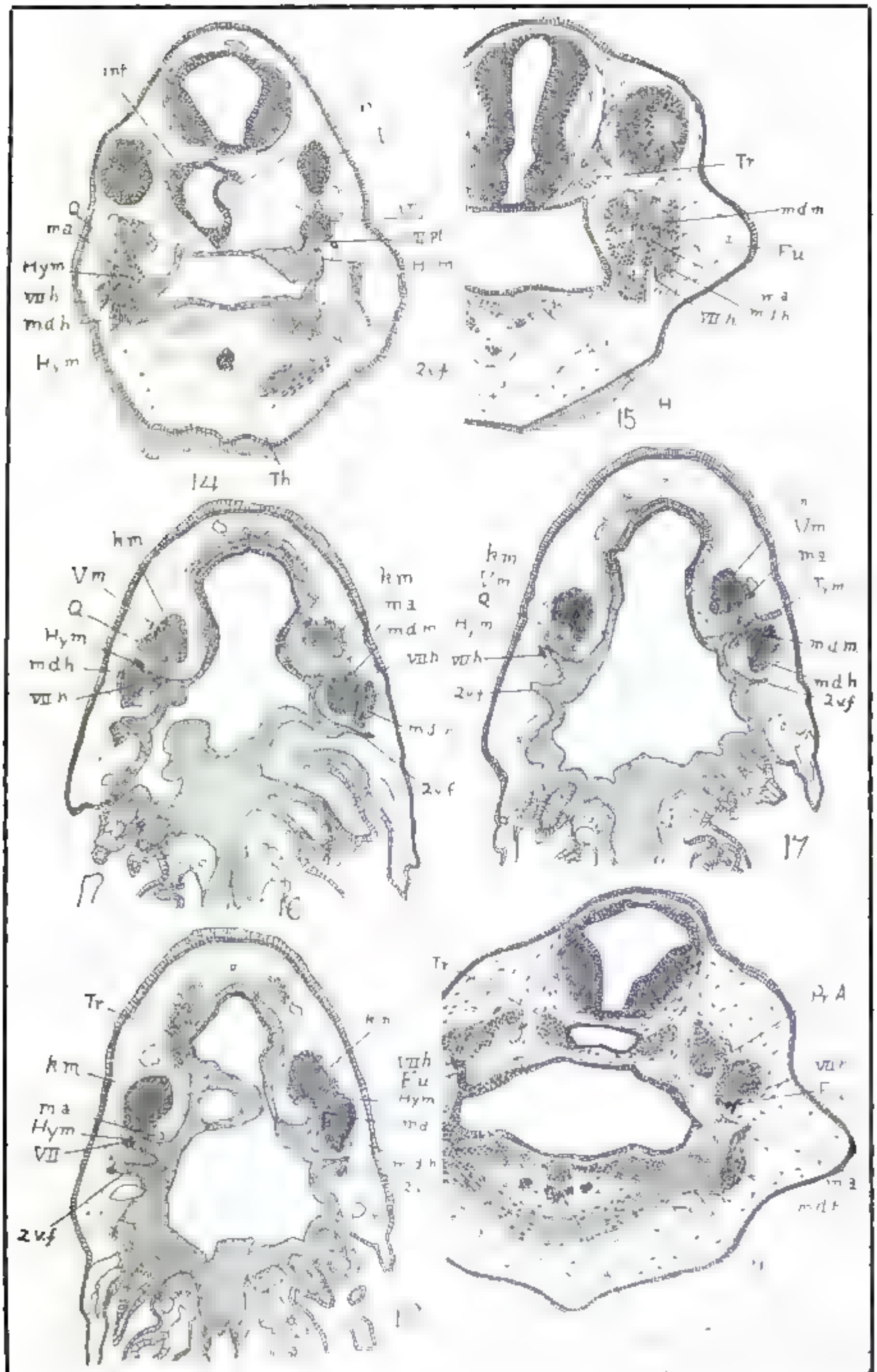

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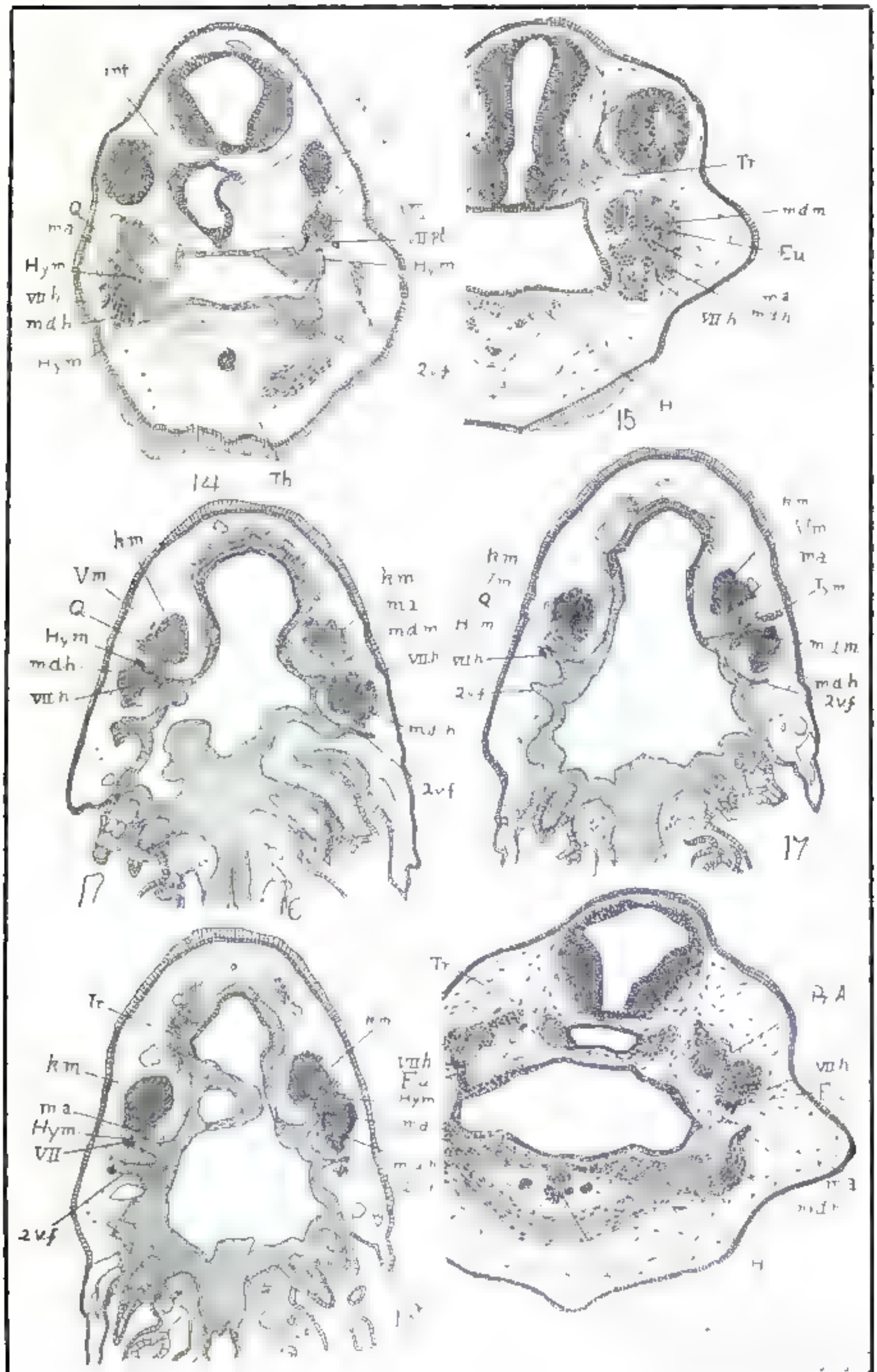

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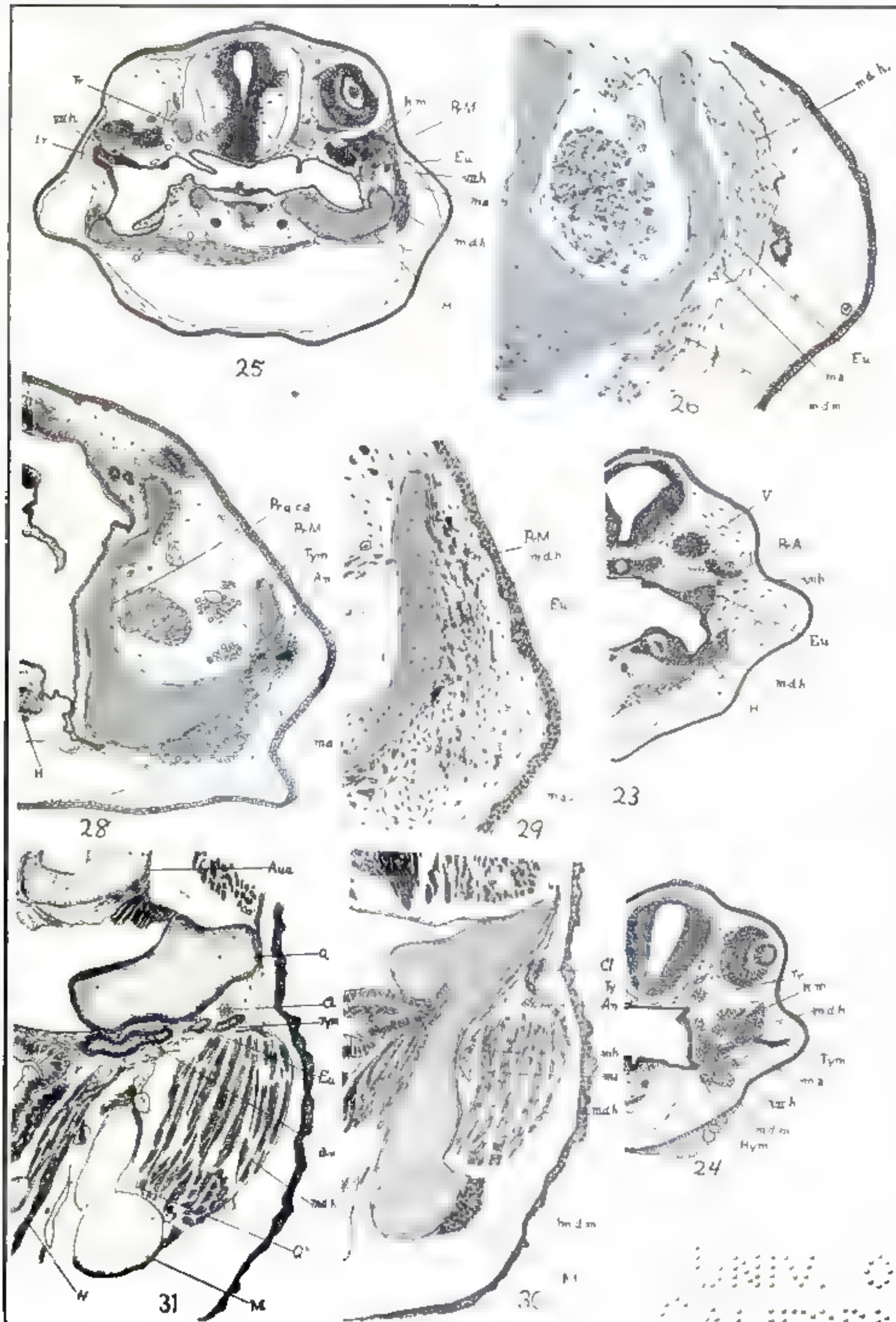

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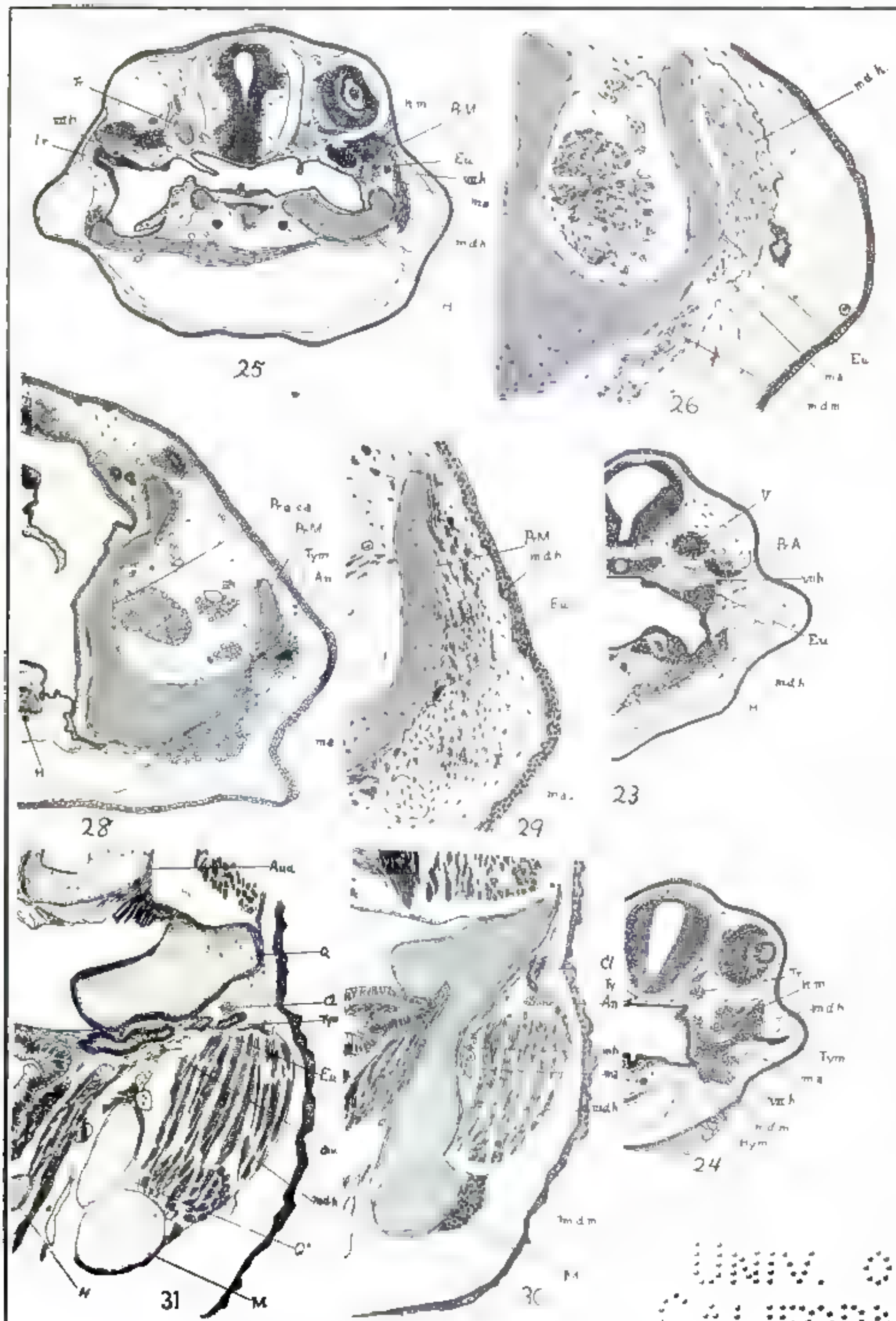

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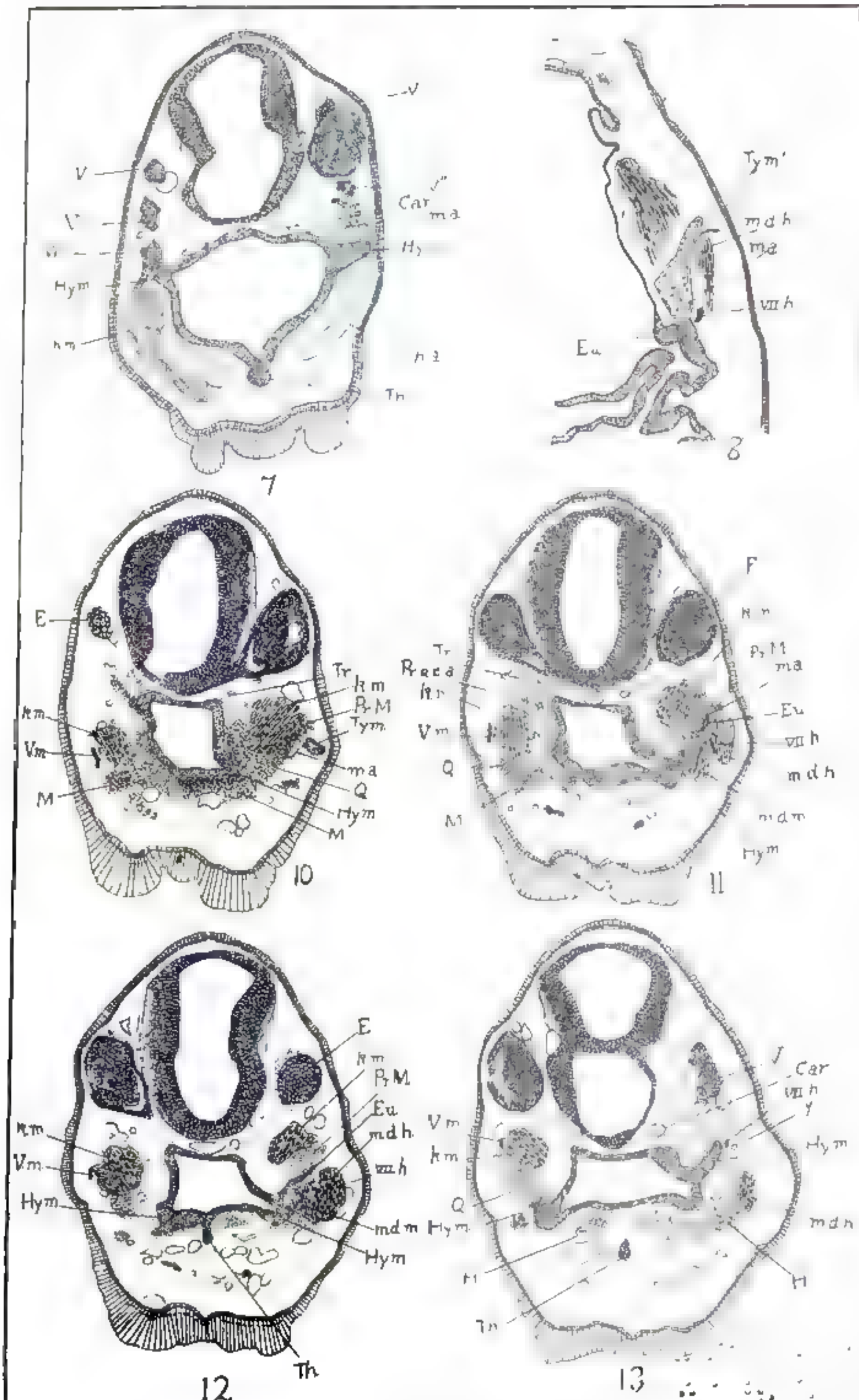

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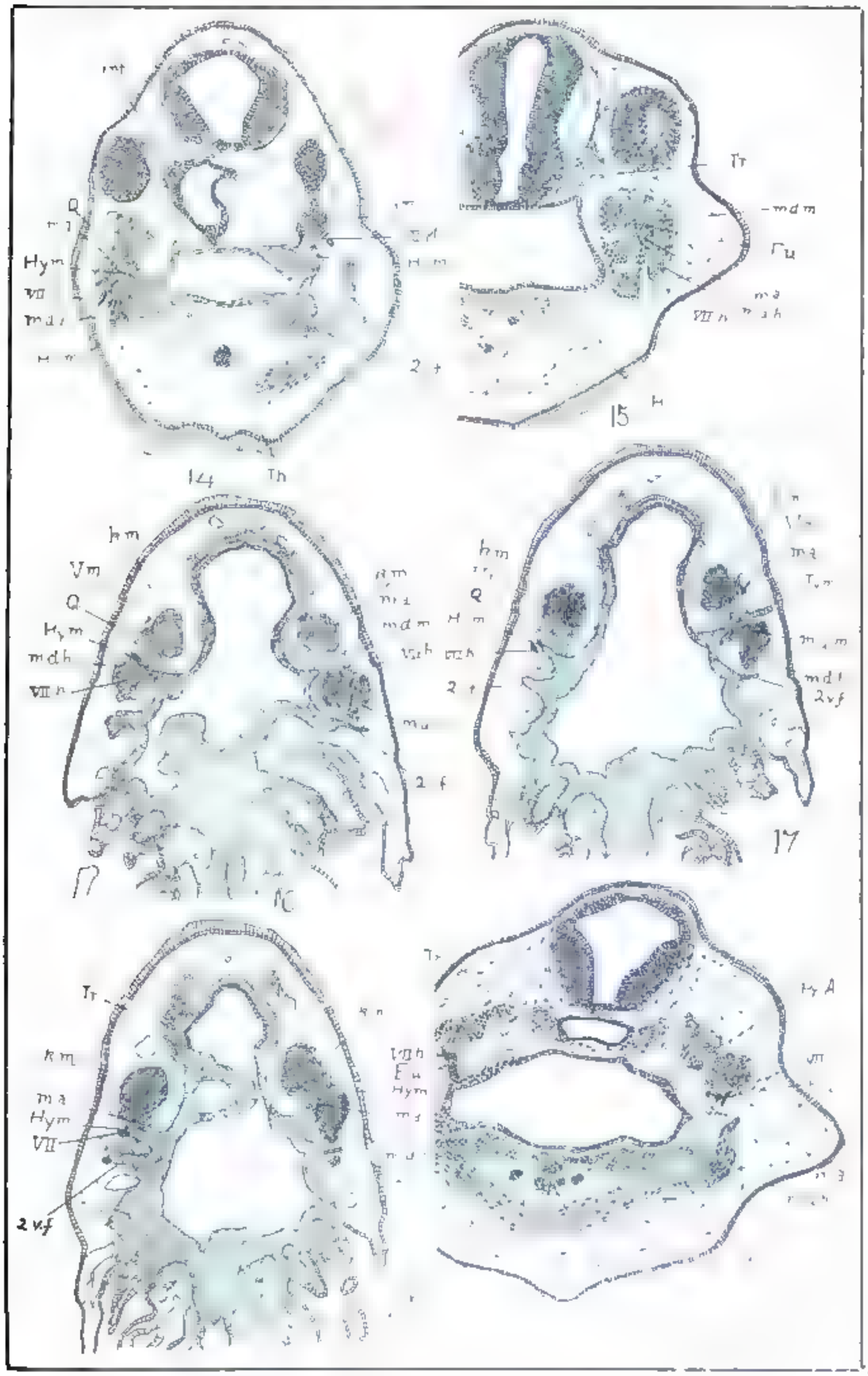

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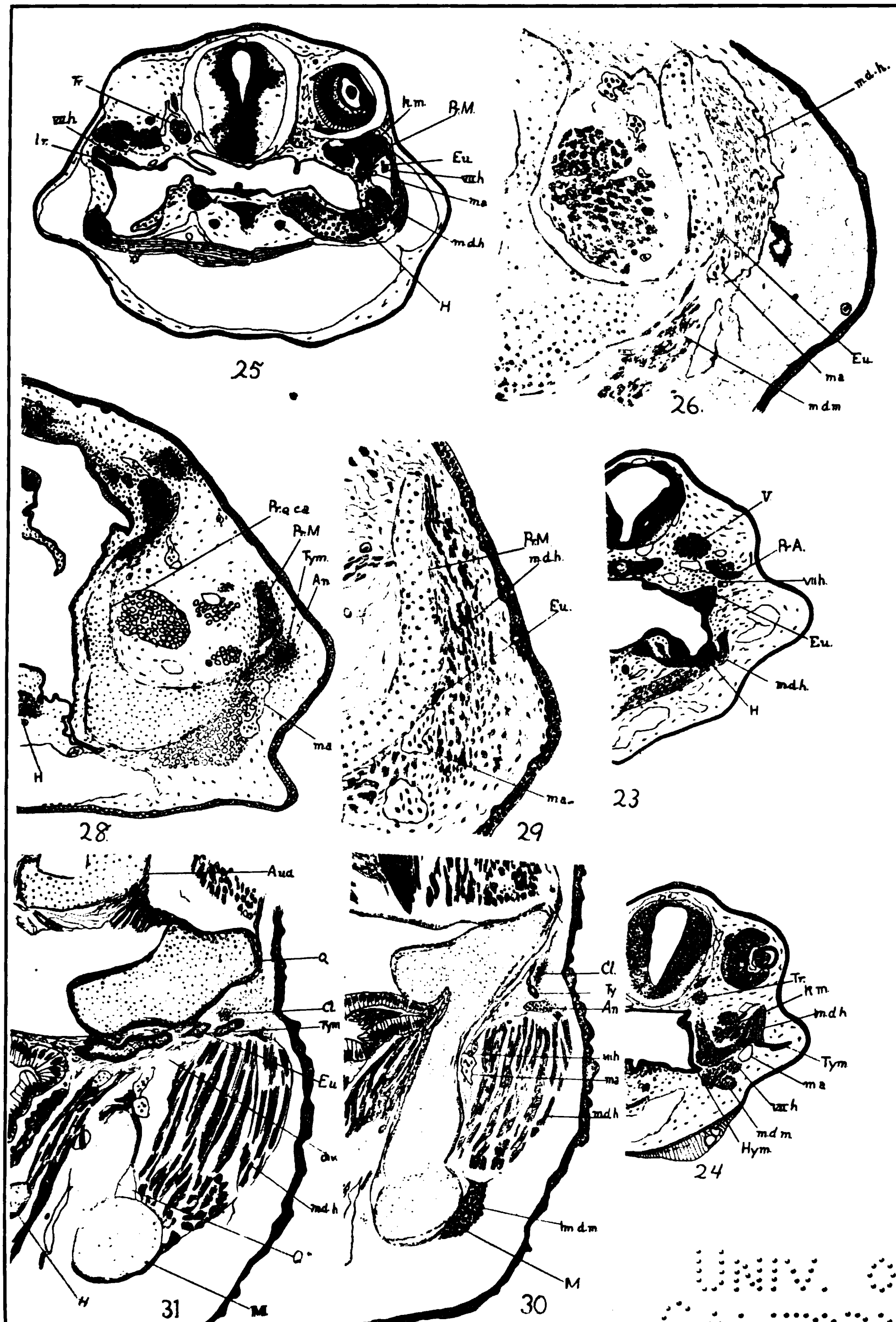

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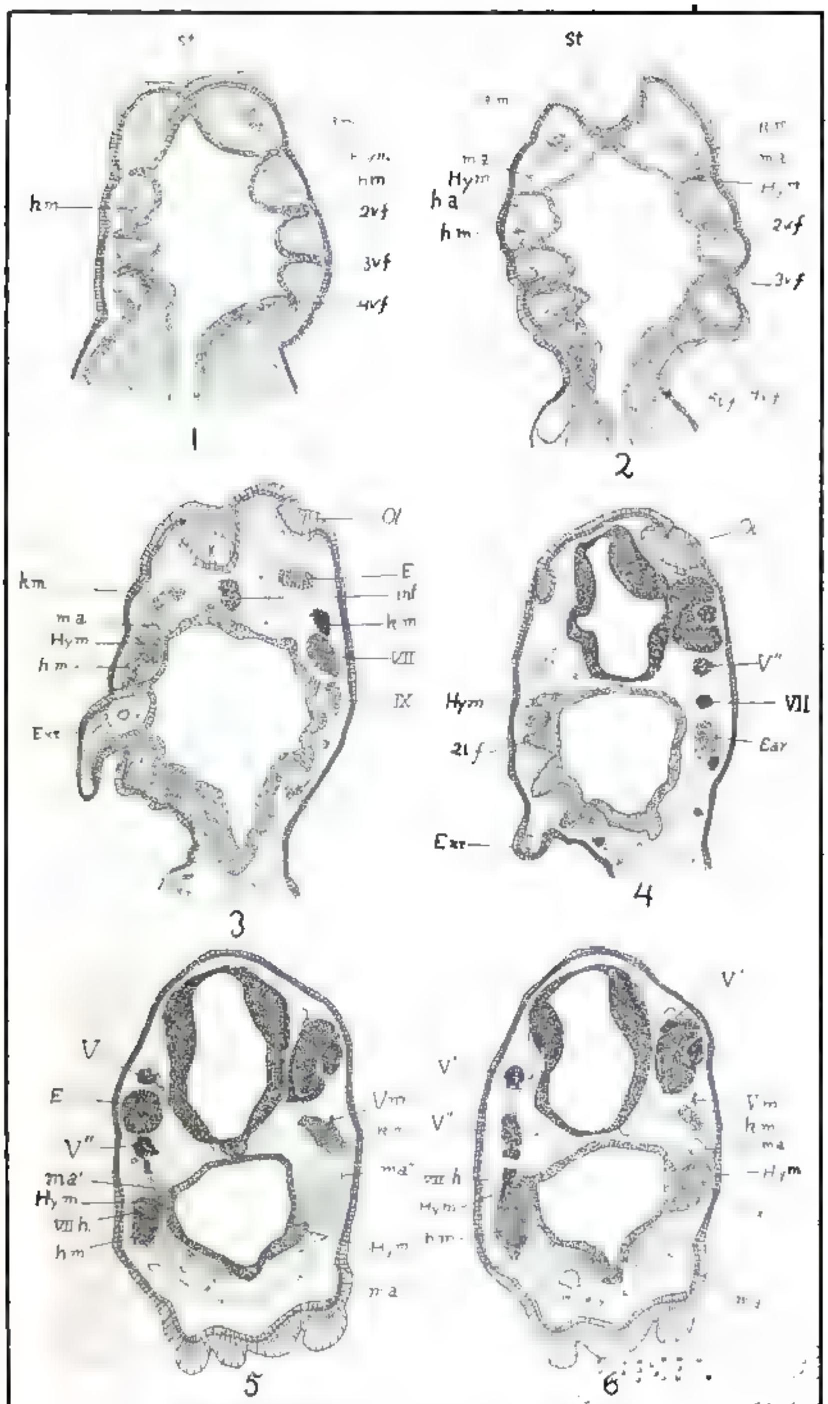

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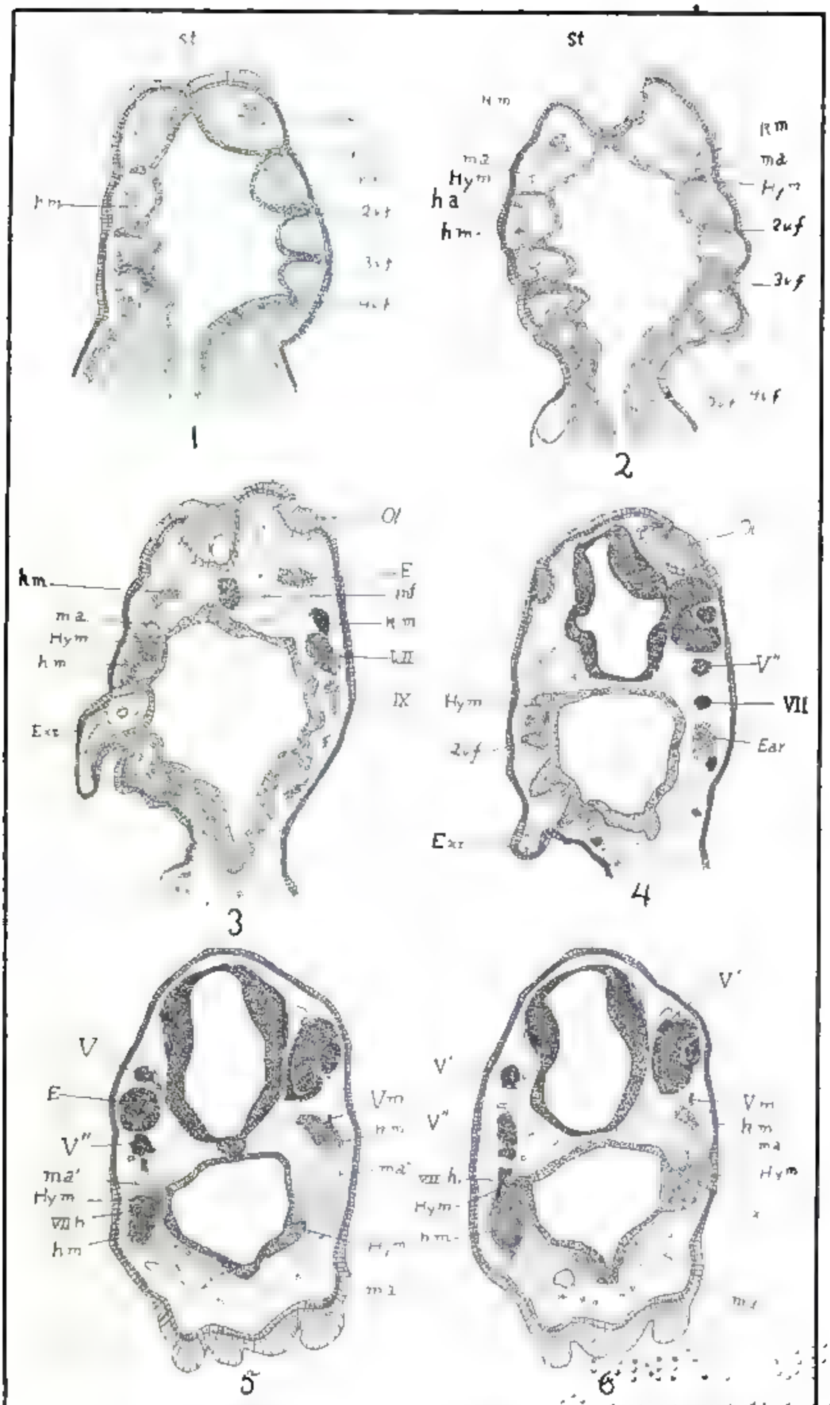

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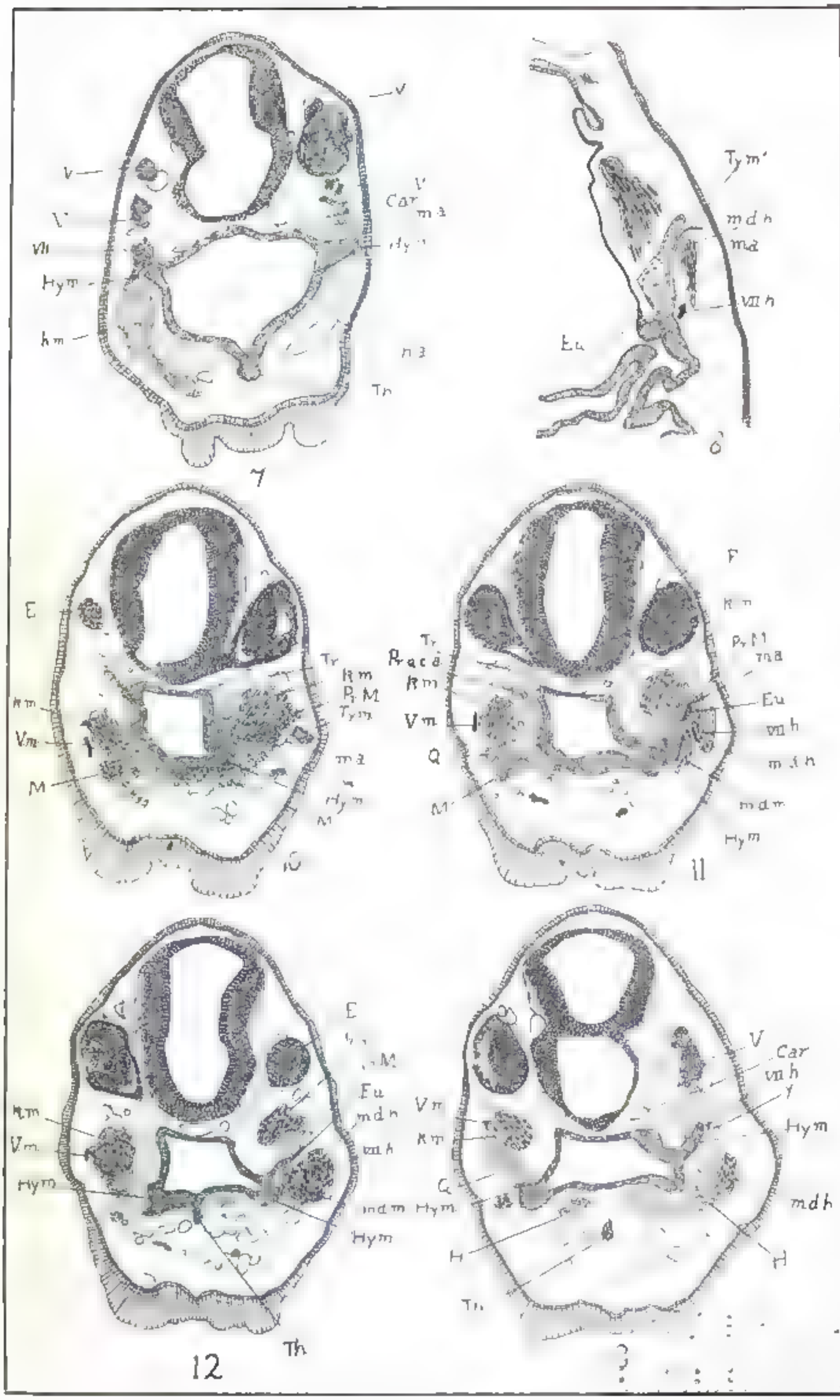

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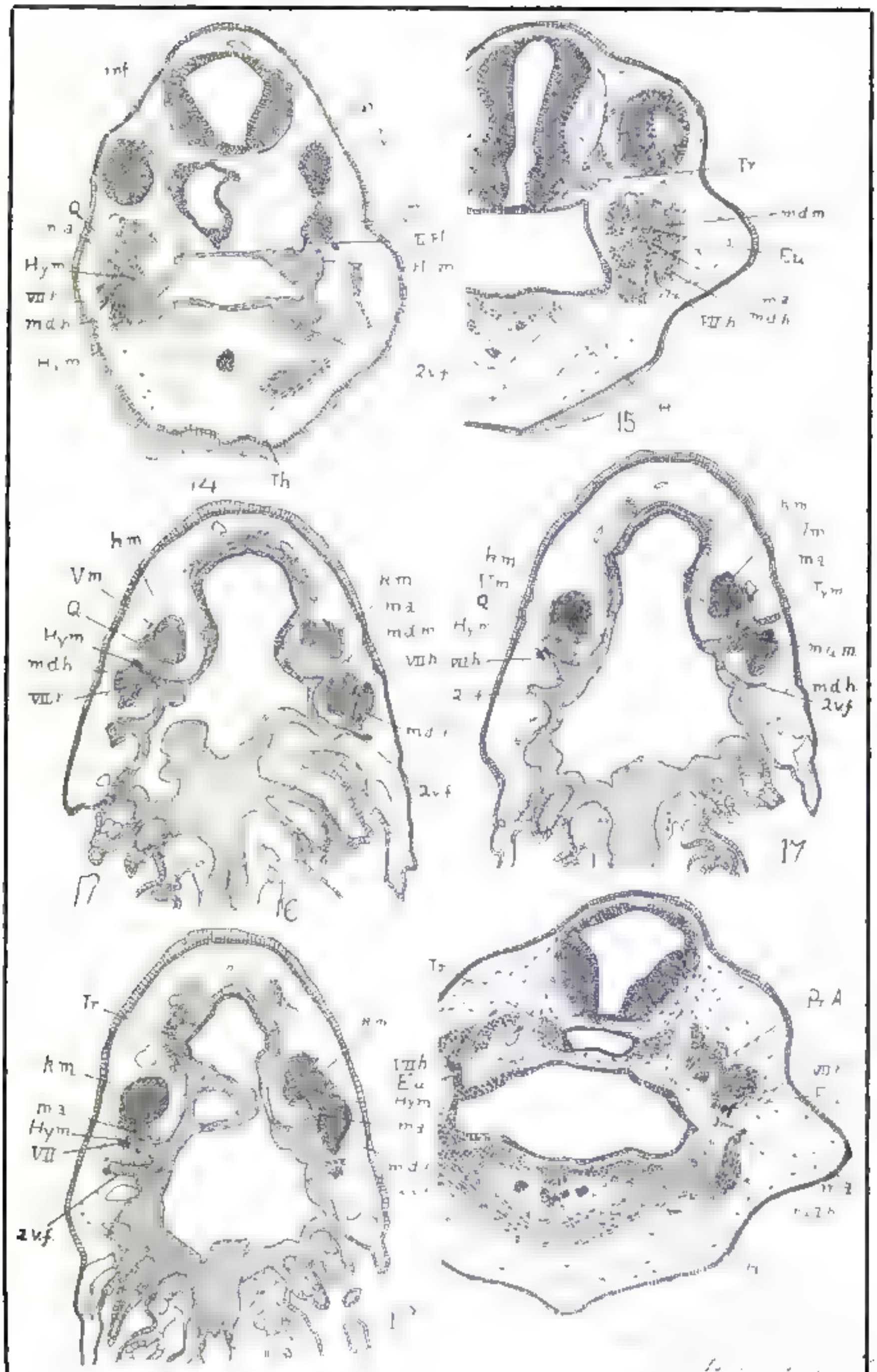

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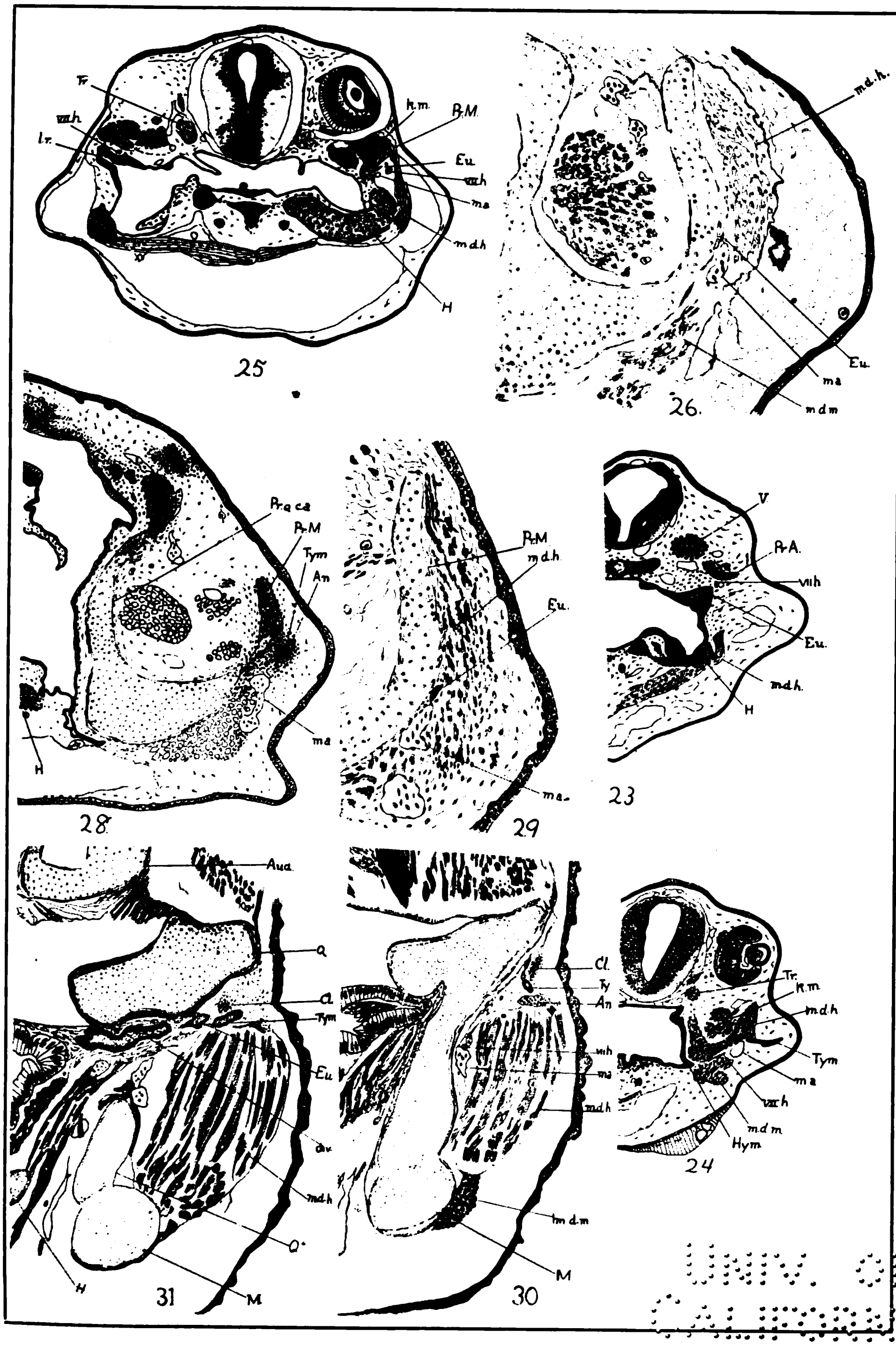

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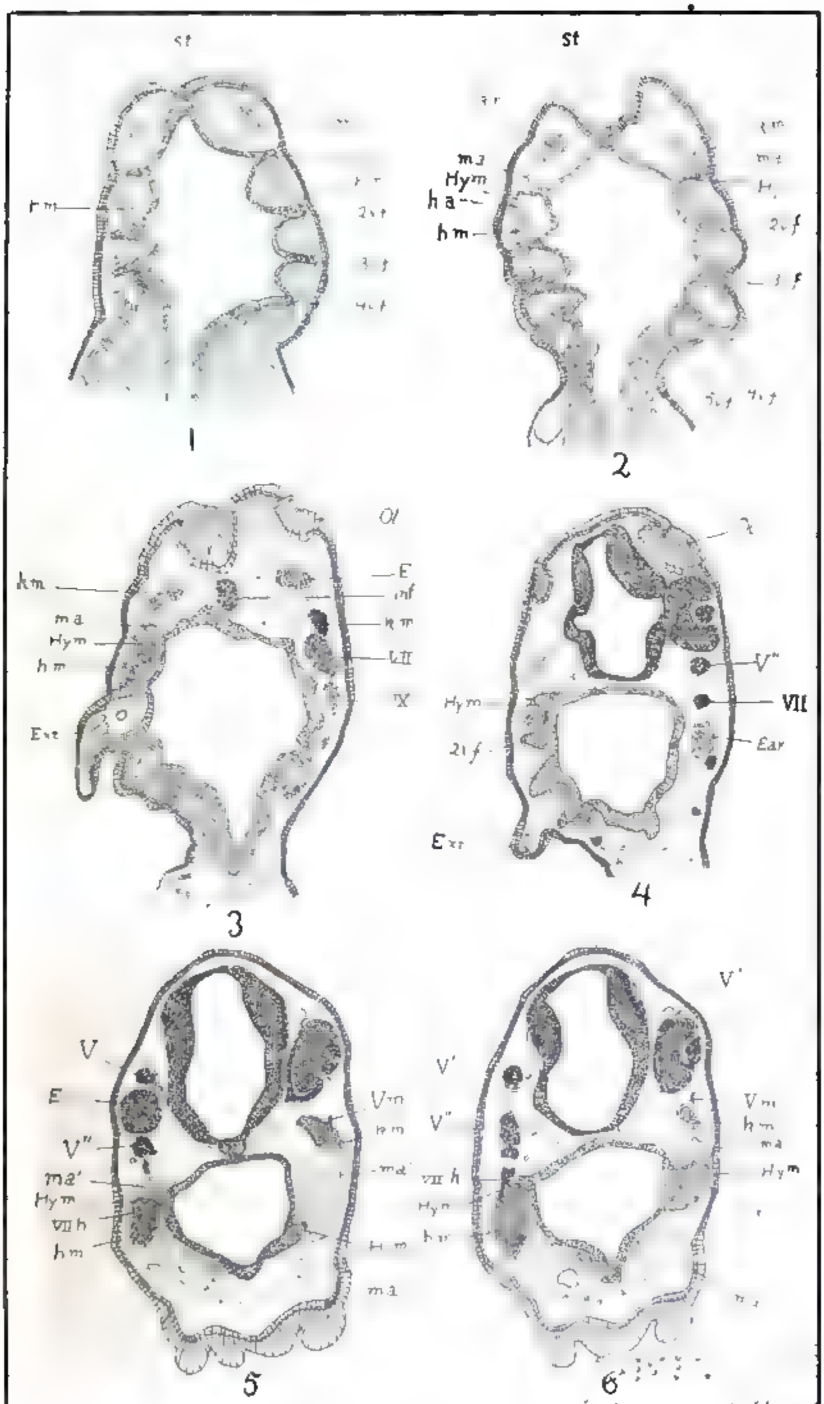

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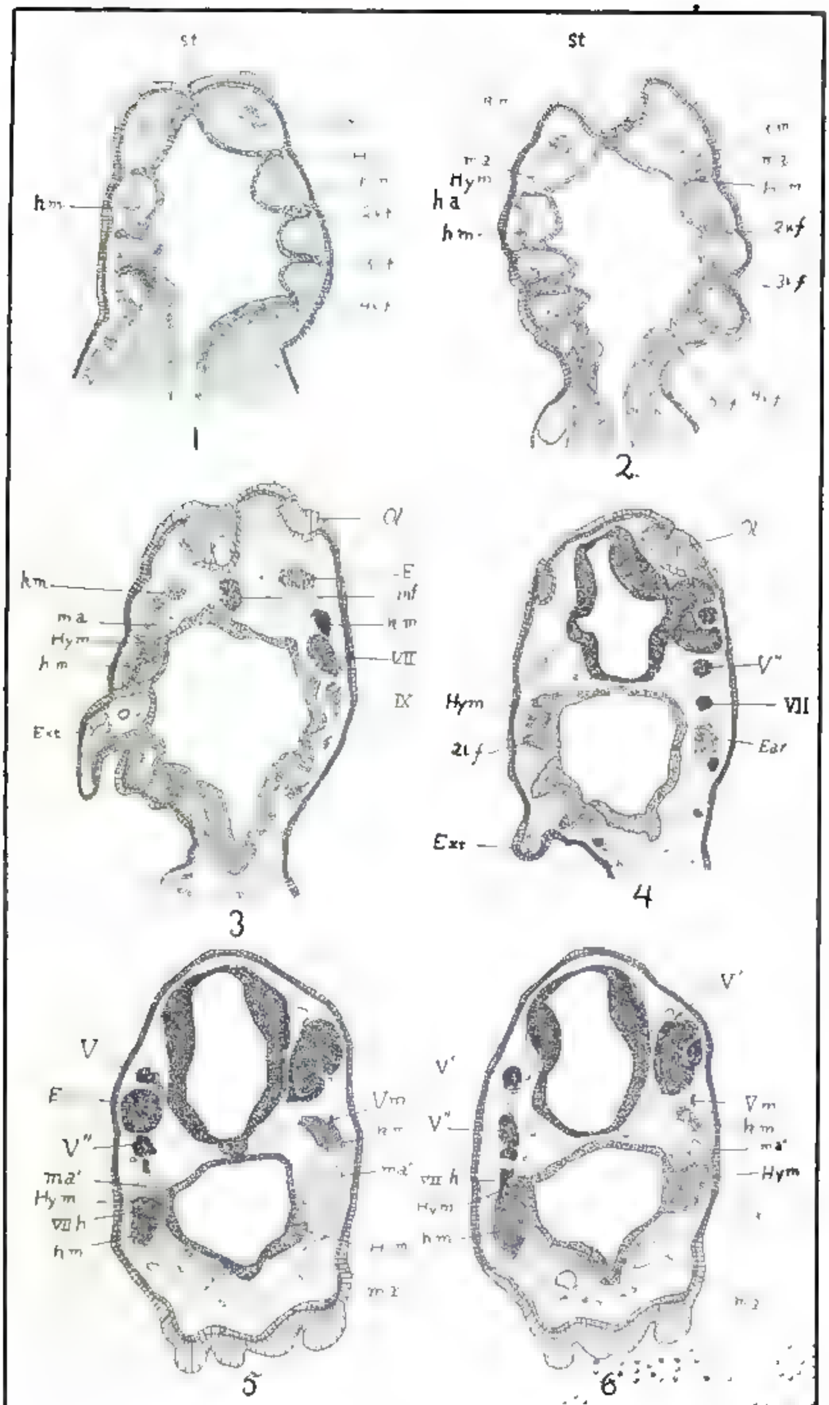

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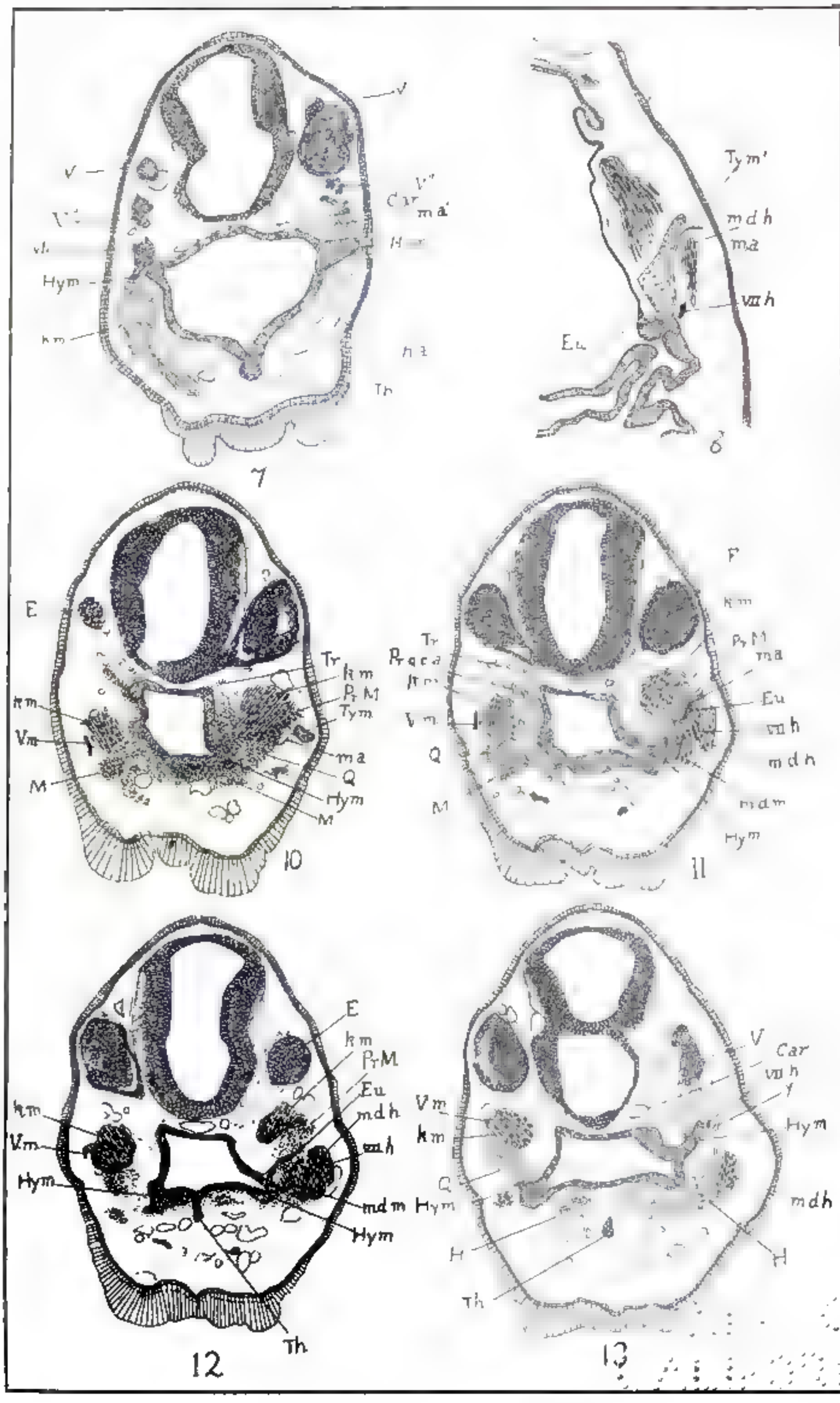

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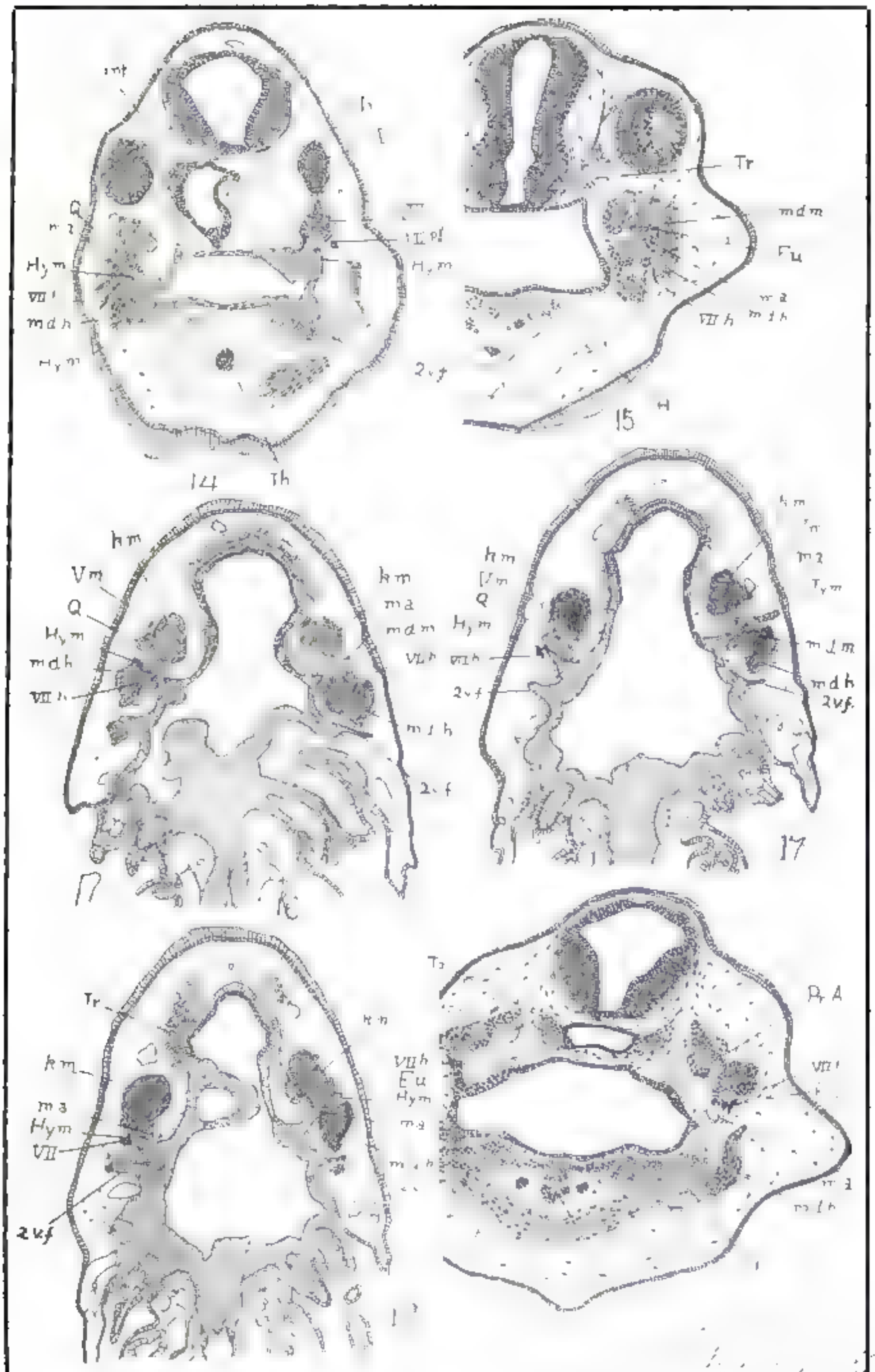

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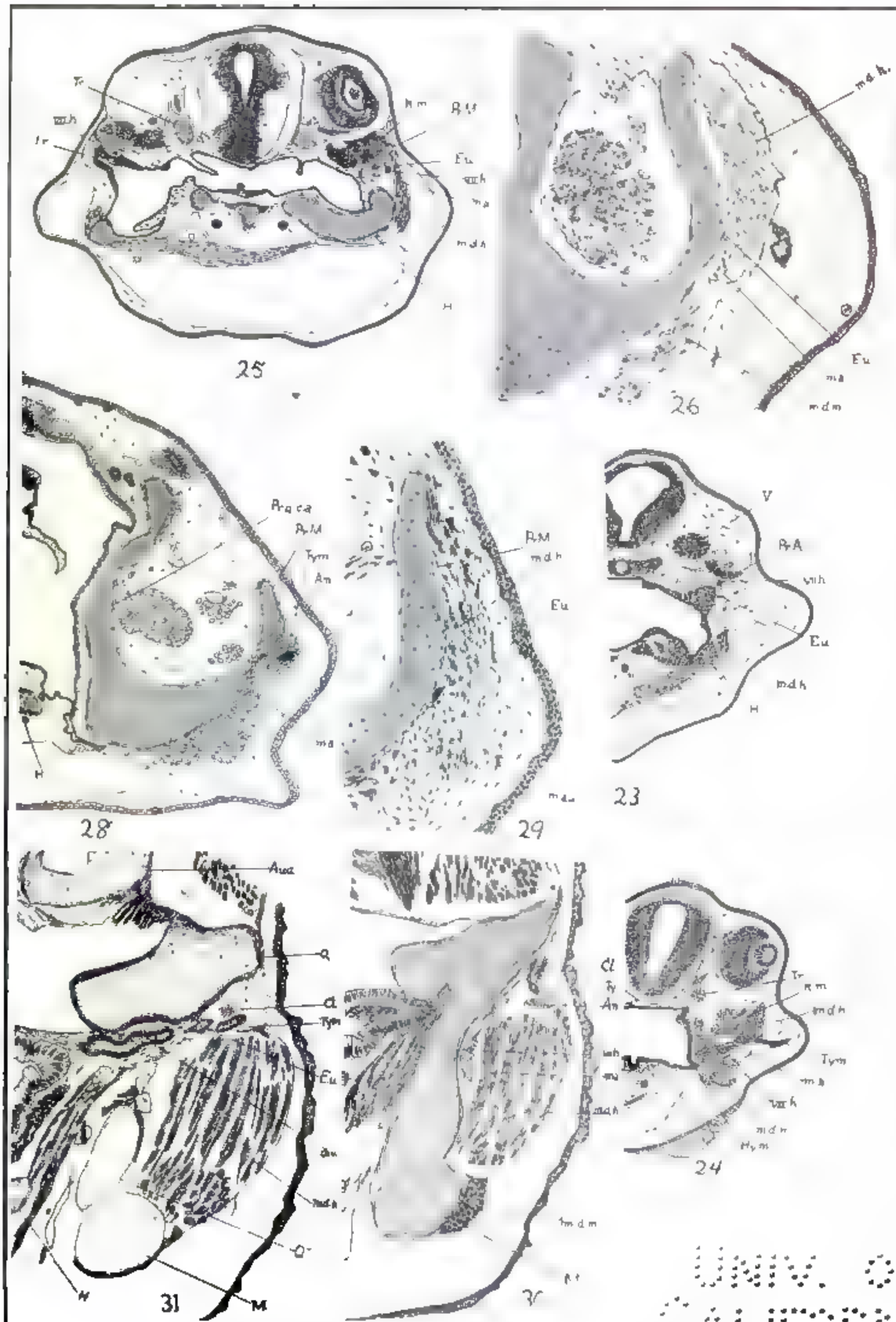

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(tadpole of about 18 mm.) I have been enabled to trace out such a connecting cord.

13. Regeneration of the tympano-Eustachian *Anlage* begins at a period immediately preceding the period when the fore-limbs break out of the opercular cavity.

14. The later metamorphosis of the tubal *Anlage* is connected with the modifications of the neighboring skeletal structures, particularly with the posterior rotation of the quadrate. By this means the tubal cord comes into relation with the auditory region of the skull and the various fragments are brought closer together, so that they can readily unite.

15. The acquisition of a lumen by the tubal *Anlage* takes place gradually, beginning at the close of the metamorphosis. Details apparently vary in different individuals.

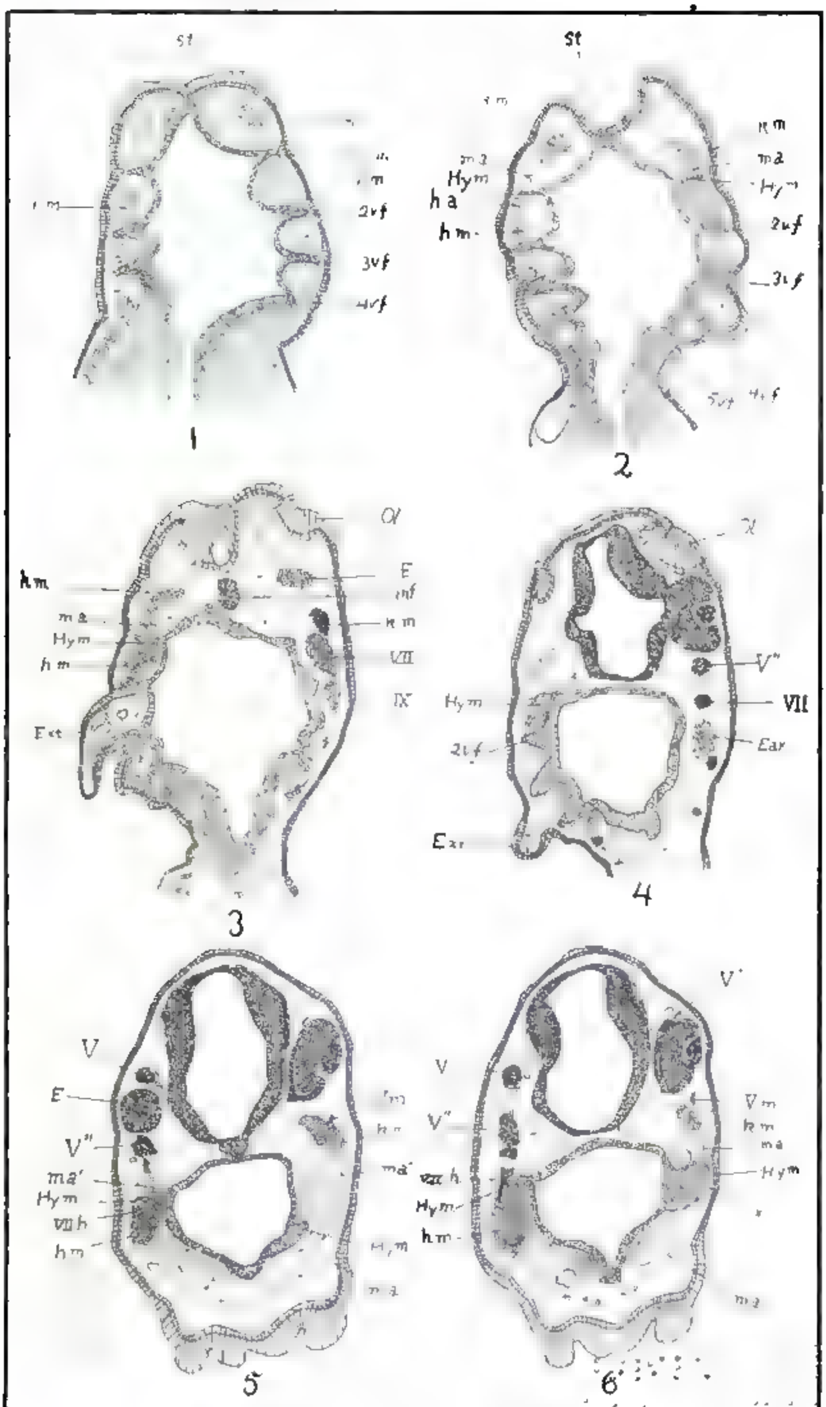
16. Completion of the tympano-Eustachian passage is effected by an outgrowth from the pharynx which unites with the tubal *Anlage*.

17. The final position of the tympano-Eustachian tube between the mandibular and hyoid bars is produced by the separation of the latter from the quadrate and its attachment to the auditory capsule posterior to the tube.

18. The annular cartilage arises at a stage immediately preceding the protrusion of the fore-limbs. Its *Anlage* forms a dense cellular strand derived from the perichondrium of the quadrate and surrounding the tympanic portion of the tubal *Anlage*. It does not begin to form fully differentiated cartilage until after the close of the metamorphosis.

19. The stapes arises within the membrane closing the fenestra ovalis. It has no connection with any of the visceral-arches.

20. The columella auris is first met with in the early stages of the metamorphosis, as a compact cellular strand extending forward from the stapes and terminating imperceptibly in the connective tissue. It continues to grow forward and acquires connection with the quadrate. Continued growth brings it in contact with the tympanic cavity. Chondrification begins in the posterior portion of the rod.



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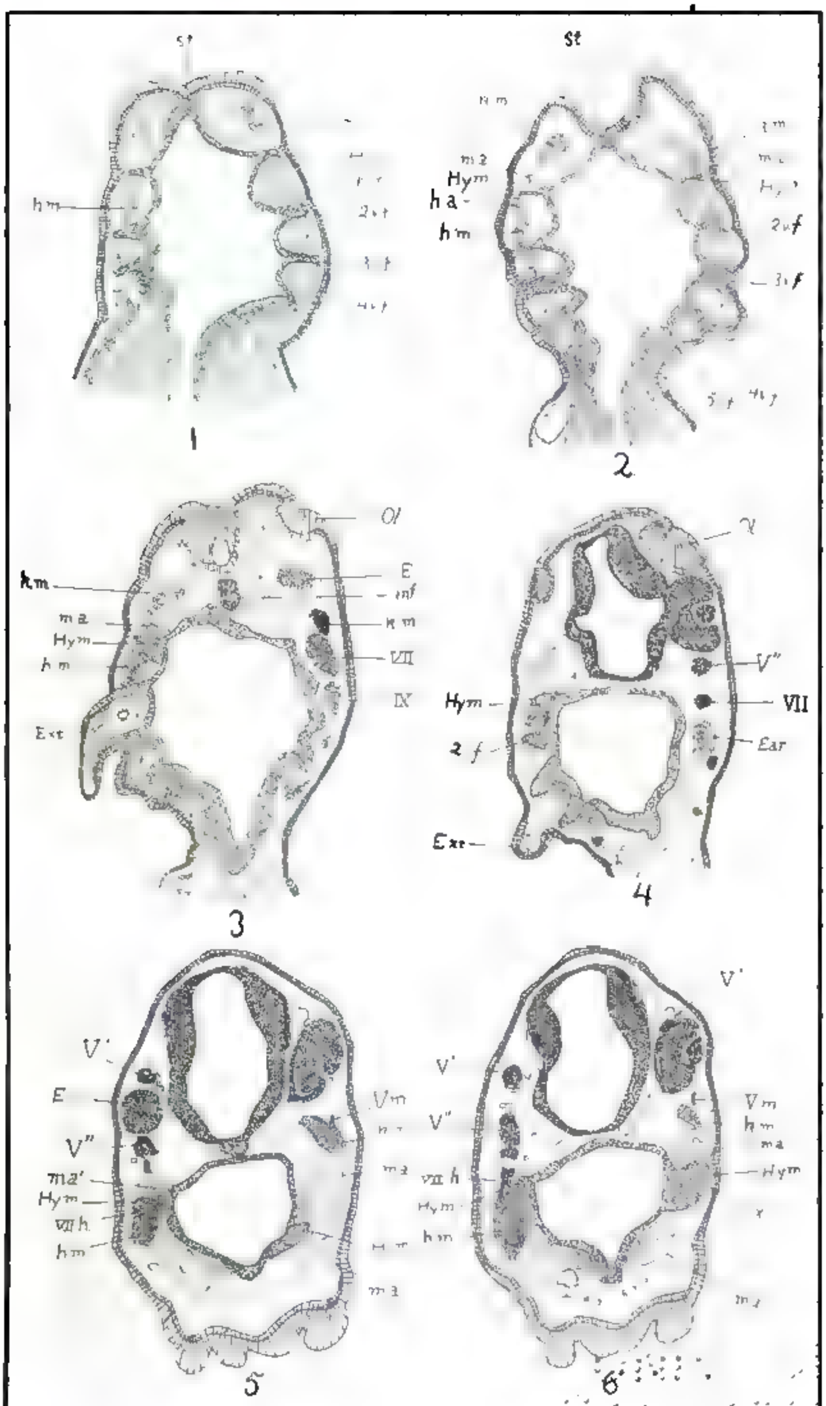

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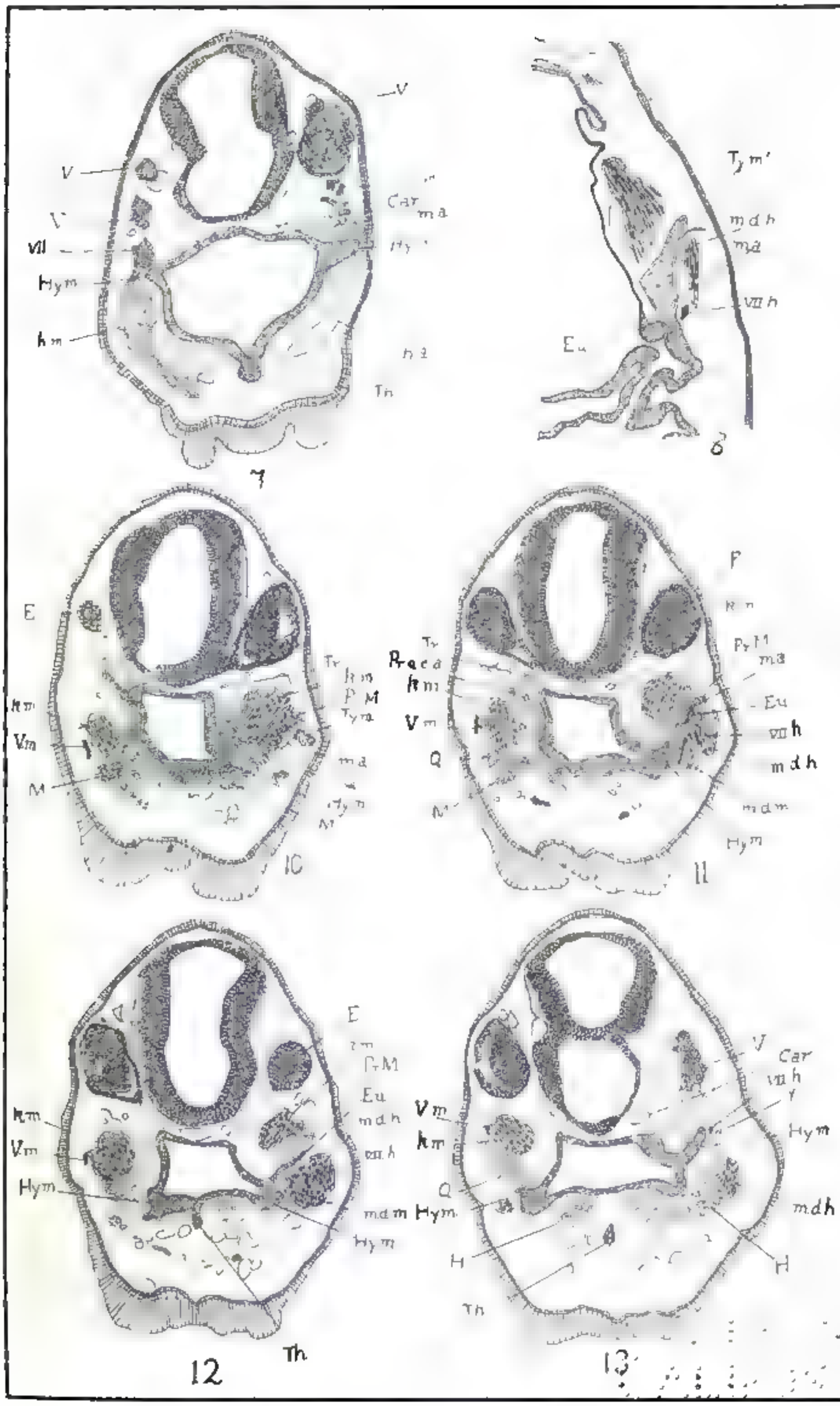

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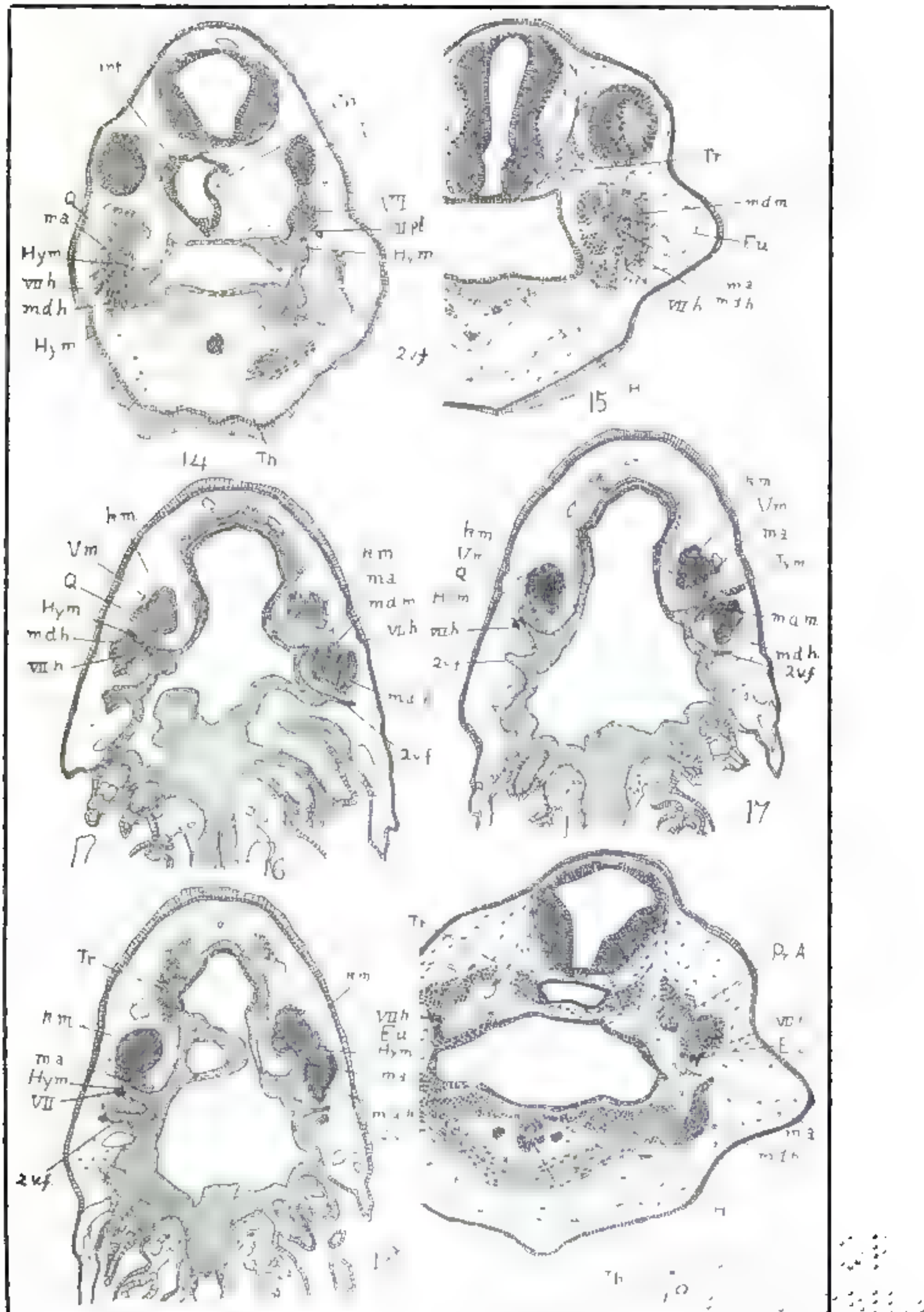

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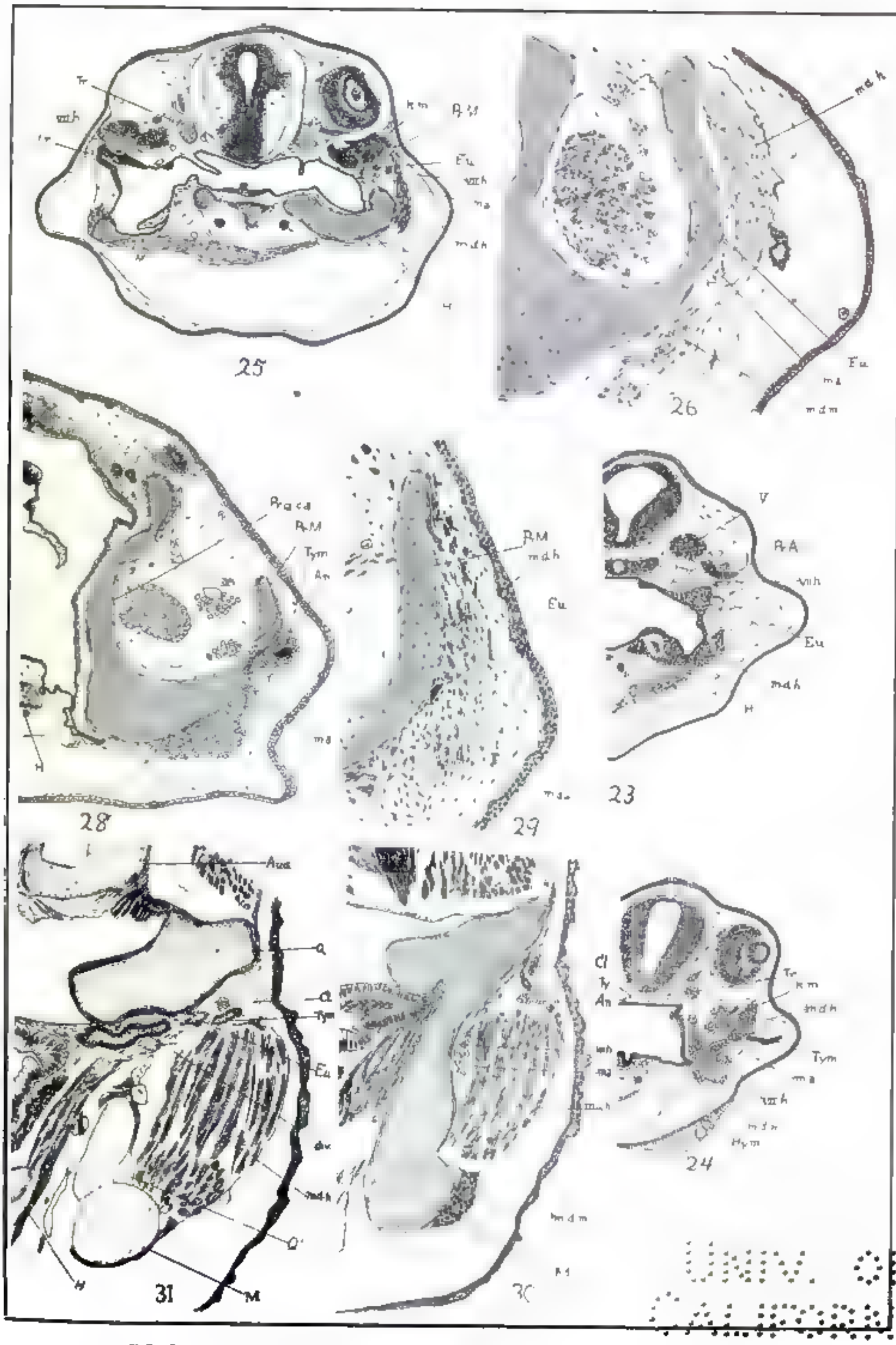

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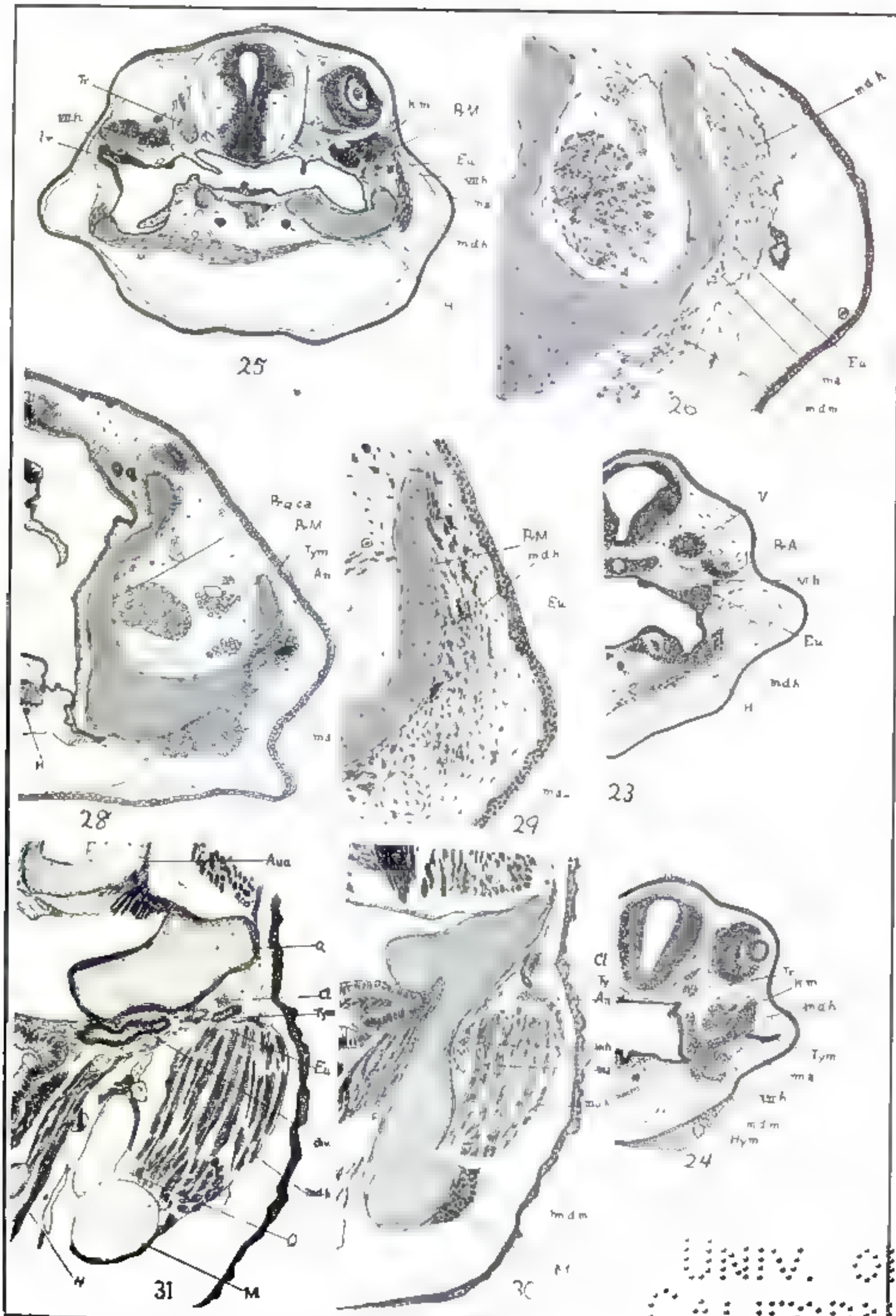

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Haughton
chordamum, Spelerpes.

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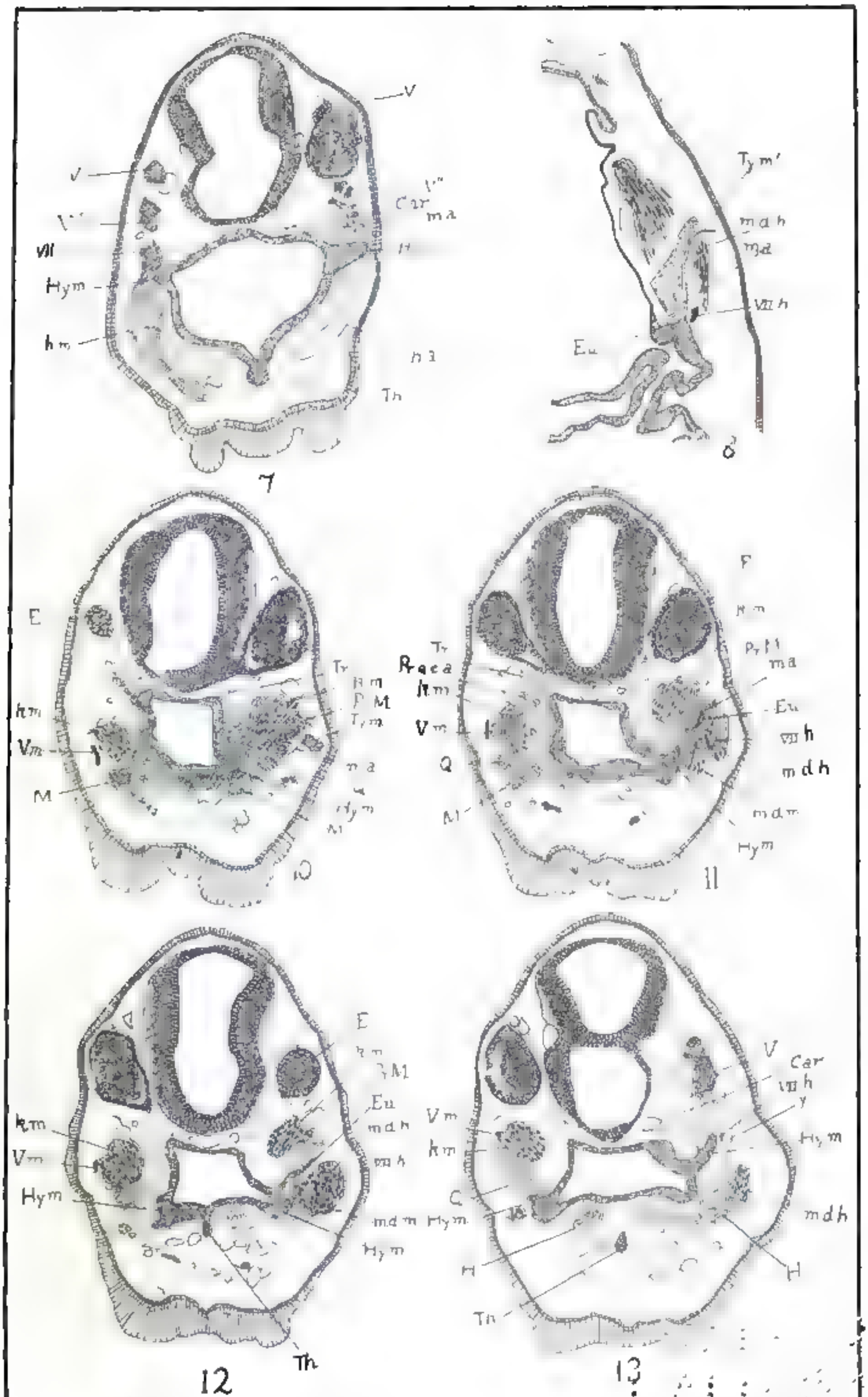

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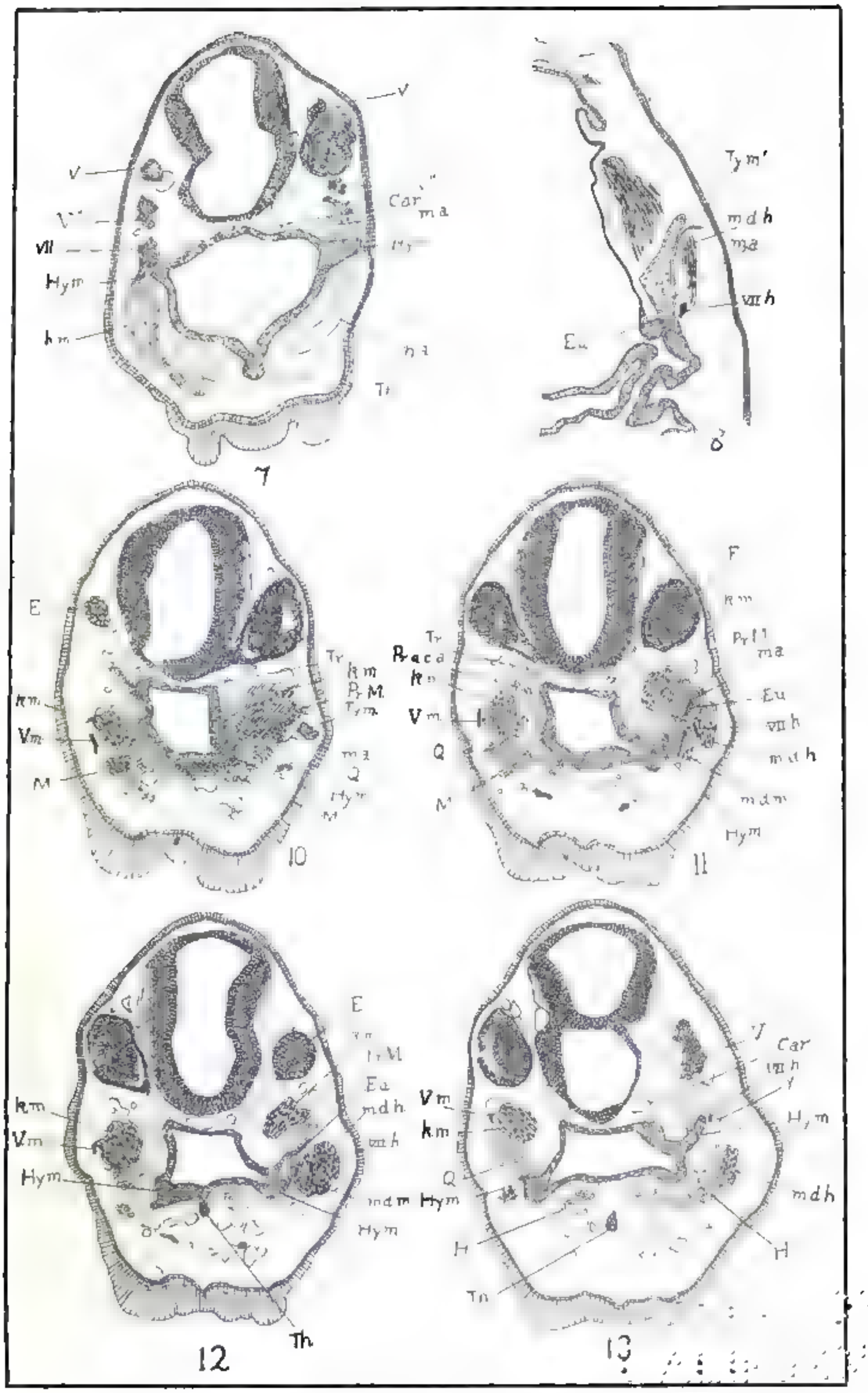

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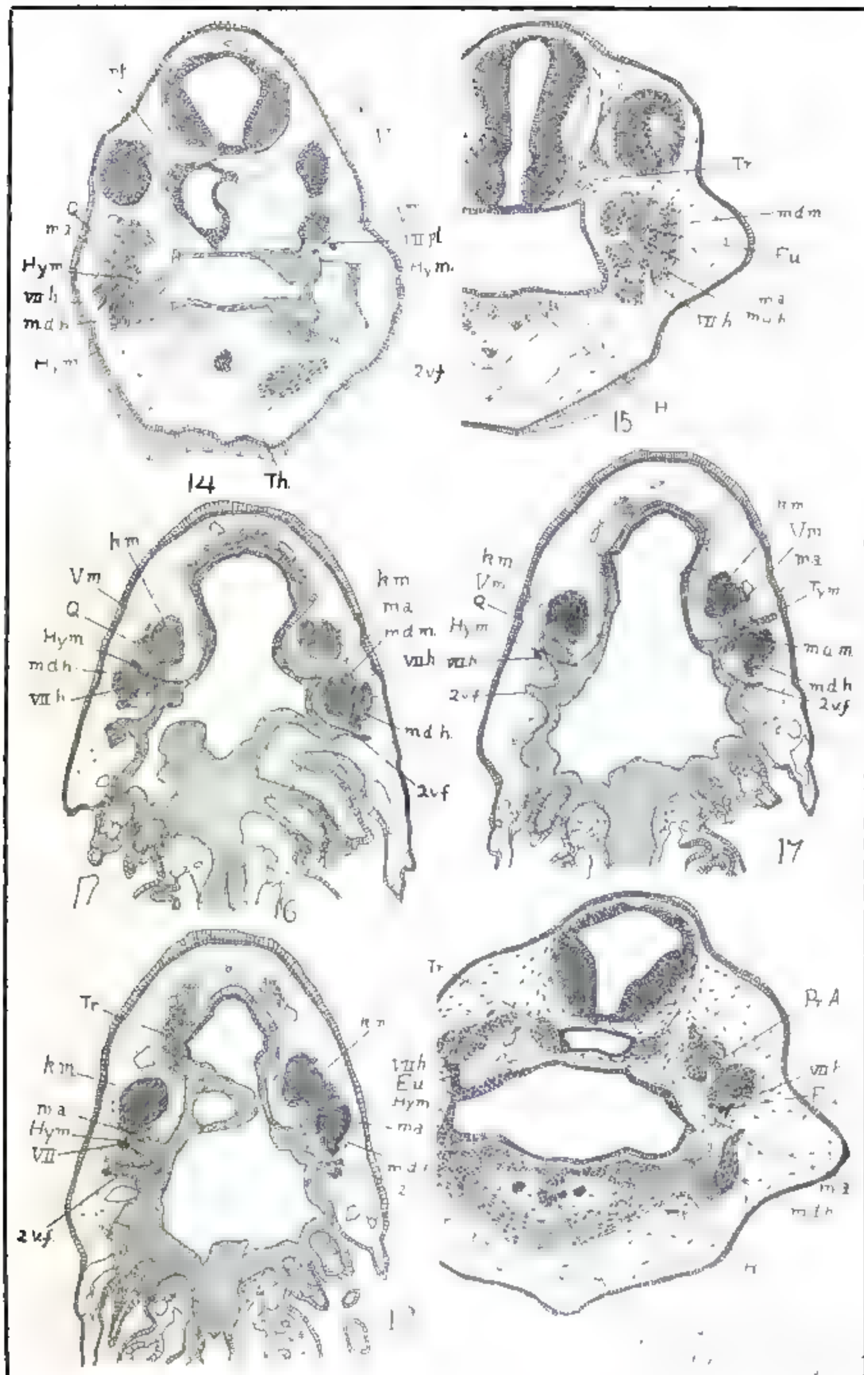

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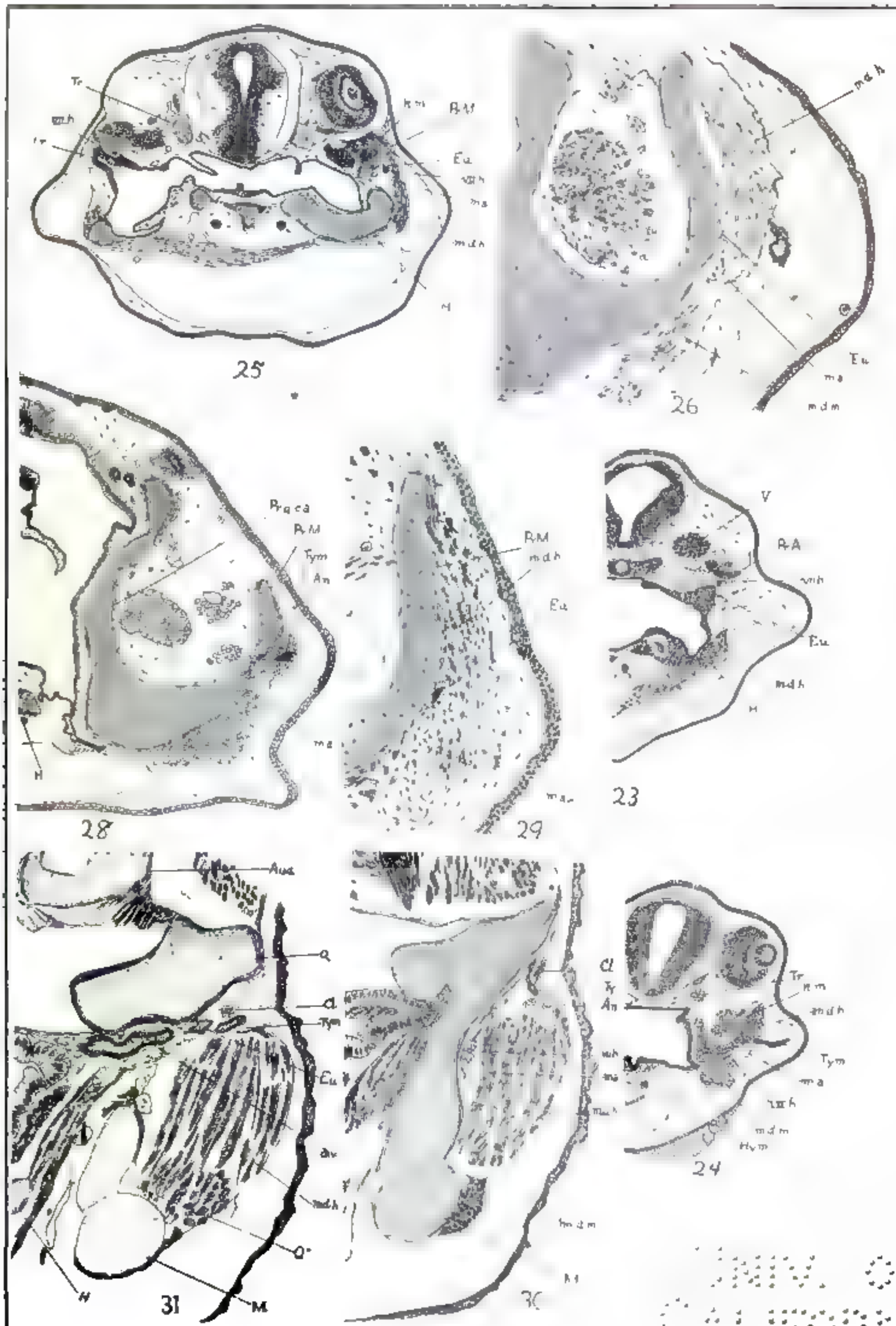

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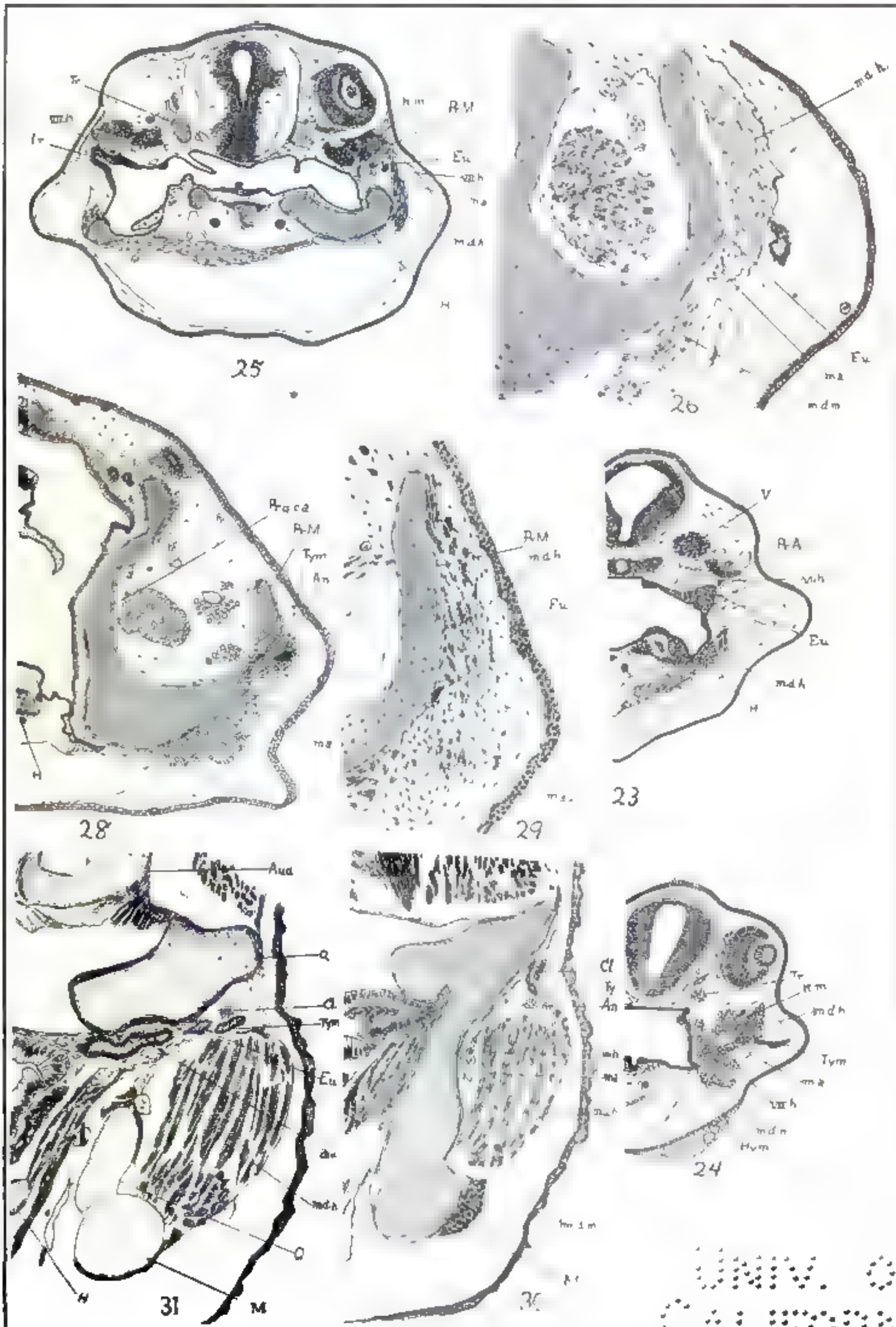

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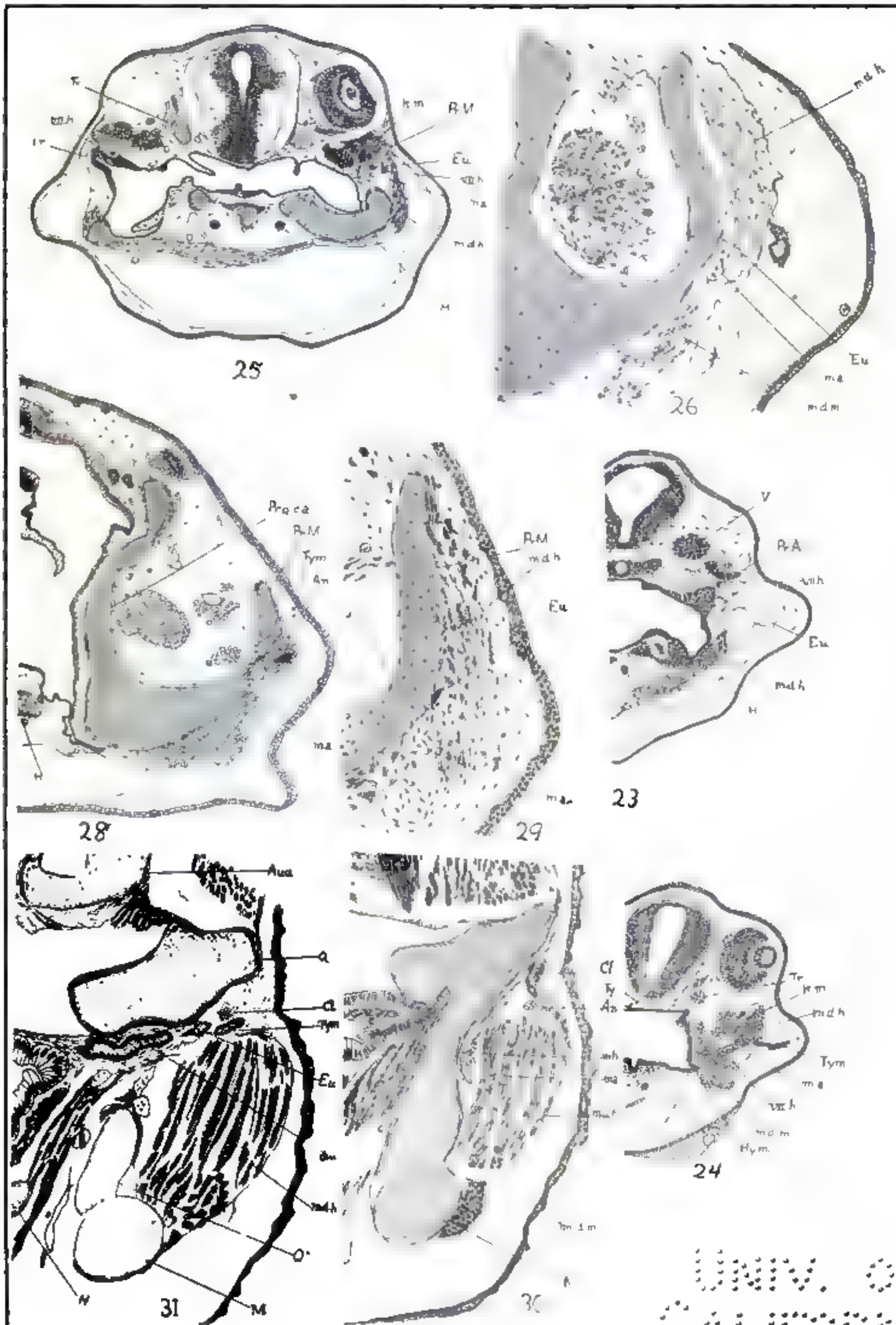

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Fig. 12.—Third section posterior to the last. The diverticulum (*Eu.*) is now continuous with the antero-inferior portion (*Hym.*) of the hyomandibular fold. Between the two is the depression lodging the muscles (*m.d.m.* and *m.d.h.*). The small vessel above *Eu.* is the mandibular aortic arch.

Fig. 13.—Sixth section posterior to the last. The mandibular aortic arch is dorsal to *Hym.*

Plate VIII, Fig. 14.—Third section posterior to last. The mandibular aortic arch on the right side is just internal to *vii pl.*

Fig. 15.—Transverse section of head of tadpole of stage IV in the region immediately posterior to that shown in figure 24.

Fig. 16.—Coronal section of the head of a young tadpole of stage II. On the right side the section passes a slight distance above the floor of the pharynx, while on the left it is considerably higher. The small vessel in front of *Hym.* is the mandibular aortic arch.

Fig. 17.—Fourth section dorsal to the last. On the right side the little protrusion of the pharyngeal wall just internal to *Tym.* is the antero-inferior portion of the hyomandibular fold just below the point where it becomes continuous with *Tym.* The space between the two is the depression.

Fig. 18.—Coronal section of the head of the same animal a slight distance below the roof of the mouth.

Fig. 19.—Transverse section of the head of a tadpole of stage IV in the region of the processus ascendens.

Plate IX, Fig. 23.—Transverse section of the head of a tadpole of stage IV, passing through a region slightly anterior to the auditory sac.

Fig. 24.—Transverse section of the head of a tadpole of stage IV, showing the anterior expanded portion (*Tym.*) of the Eustachian cord. *Hym.* denotes the proximal anterior portion of the hyomandibular cleft.

Fig. 25.—Transverse section of the head of a tadpole of stage V. On the left the section is immediately posterior to the eye. The minute upgrowth from the dorsal wall of *l.r.* just internal to *vii h.* is the Eustachian proliferation.

Fig. 26.—Transverse section of a portion of the right side of the head of an old tadpole of 18 mm. (stage VI). This section is considerably more magnified than the others and is intended to show the extremely rudimentary character of the Eustachian cord at this stage.

Fig. 28.—Transverse section of the right side of the head of a tadpole at the beginning of the metamorphosis (stage VIII), showing the formation of the annular cartilage.

Fig. 29.—Transverse section of a portion of the right side of the head of the same animal. The section was drawn with the same degree of magnification as figure 26 and is intended to show the Eustachian cord when it begins to regenerate.

Fig. 30.—Transverse section through one side of the head of a young toad (stage XV). The section passes through the region immediately in front of the ear-capsule.

Fig. 31.—Transverse section through one side of the head of the same animal. The section passes through the anterior portion of the ear-capsule.

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TABLE OF CONTENTS.

MUSCULAR AND SKELETAL ELEMENTS IN SPELERPES LONGICAUDUS.*

HENRY SPENCER HOUGHTON.

The development of one of our commonest species of Salamander affords an opportunity for the study of many interesting problems. The author was influenced, however, in taking up a study of the skeletal and muscular elements in Spelerpes longicaudus, by several considerations. In the first place, there is a surprising lack of literature, especially on the latter subject. The question of the origination and development of adult muscles and of the number and function of transitory larval muscles, and of the relation of the two, seems to have been entirely neglected. The skeletal elements have been thoroughly worked for the adult form, but there are some modifications in the larval skull that have not been touched upon. Secondly, this form is abundant, of wide distribution, and readily obtainable, and this fact together with the facility with which it may be prepared, renders it valuable material for laboratory purposes. The work was done in the Embryological Laboratory of the Ohio State University, under the direction of Professor F. L. Landacre, and was offered as a thesis for the Baccalaureate degree.

This paper will attempt to cover merely a discussion of the skeletal and muscular elements of a 12 mm. larva, and will be for the most part descriptive, a few comparisons only being drawn with Rana and Cryptobranchus.

Spelerpes longicaudus is one of the commonest and most widely distributed species of the Plethodontidae. Its general appearance and markings are similar to Sp. bilineatus, and they are commonly found associated together in nature. Their habits, larval development and the noticeably longer tail of Spelerpes longicaudus form, however, distinguishing marks. The larval development of Sp. bilineatus is much more rapid than that of its relative; a 9 mm. specimen which I observed had both fore and hind limbs

*Contribution from the Department of Zoology and Entomology, IX.

fully formed, while a 12 mm. Sp. longicaudus has merely limb buds, scarcely distinguishable to the naked eye. Of its habitat, Cope says: "This beautiful animal is not very active in its habits and is almost always found in rocky ground and in fissures and caves in cliffs." (Batrachia of N. A., p. 154.) This species is scarcely ever found in water save in the breeding season, while Spelerpes bilineatus abounds in rocky brooks. The larvae may be found in open water, but at an early age they show an instinct for concealment, and are more readily found under leaves and pebbles lying in the pool.

EGGS.—The eggs of Spelerpes may be found most abundantly in May and June. "They are deposited in a single layer upon the lower side of submerged stones, each batch containing from thirty to fifty eggs. The stones which are suitable for this purpose must be in the form of an arch allowing the water to flow beneath. They are generally in the more rapidly flowing portions of the brook, but the depth of the water must be such that the eggs are at all times entirely submerged, as otherwise the dash of the ripples striking against them would subject them to mechanical injury." (H. H. Wilder, "American Naturalist" Vol. XXXIII, p. 231.) The eggs are attached to the under surface of the rock by means of a gelatinous envelope in which they are encased; the same envelope keeps the eggs separated from each other much as in the case of frog's eggs.

LARVA.—The larvae of Spelerpes longicaudus are hatched somewhat early and continue for some time in the larval form. The larva at 12 mm. has the gills well developed, partially covered by an opercular fold. The tail is long and tapering, with a broad, delicate and rounded fin. The pigment is well distributed over the upper surface of the tadpole, but is lacking on the under surface, except for a few cells on the fin. The pigmentation is continuous over the anterior part of the head, but under a lens shows a double row of unpigmented areas along the dorsum, beginning behind the eye and running close to the fin. There is very little change in pigmentation at metamorphosis, as the following description of the pigmentation of the adult will show: " * * * generally * * * more thickly crowded along the sides, sometimes forming a distinct spotted band along the sides of the tail; these black bands are generally aggregated into a series of vertical bands. In younger specimens * * * the spots above are arranged in three irregular lines, one median, and two lateral larger ones. The muzzle and entire under parts are immaculate." (Cope, Batrachia of N. A., p. 154.) The pigment spots appear as brown or grayish blotches of irregular contour. The anterior and posterior limbs may be noticed as small buds, just posterior to the gills and anterior to the anus, respectively.

TECHNIQUE.—The specimens were killed and hardened for four weeks in 4 per cent. Formalin. After taking the two grades of paraffin, they were cut (.03″) and lightly stained in a Delafields' Haematoxylin, after which they were washed and ripened in water for 48 hours. This process gives a thoroughly discriminative and brilliant stain, which is admirably adapted for all classes of such material for general purposes. Three series were made, one being the stage studied, and the other two serving as checks on the first. The reconstructions of the skull were plotted in the following manner: a micrometer eyepiece was calibrated, arbitrarily, to co-ordinate paper; then the lens of the eye of the specimen, which is practically spherical, was measured vertically and the distance marked on the co-ordinate sheet. The number of sections in which the lens appears was next carefully noted, and thus the ratio of longitudinal to vertical measurements on the co-ordinate paper was obtained. This ratio was found to be 15 horizontal to 22 vertical. By calling the ratio 5.7, therefore, and adding one section to every 21 read, accurate results were obtained, and a perfectly proportioned plot drawn. Plates 8, 9, 10 were outlined with a camera and filled in by freehand.

OSTEOLOGY.—The skull of the 12 mm. tadpole of Spelerpes longicaudus differs radically from the adult skull, and shows close resemblance to the adult skulls of some lower forms. Wiedersheim lays down the general characteristic visceral skeleton of Urodeles as follows: "We may consider the ground form, as present in the larva, to consist of five pairs of bars. The anterior pair, or hyoid, consists of two pieces, as do also the first two branchial arches. The third and fourth branchial arches are much smaller and are connected with their fellows of the opposite side by a single or double basal piece. At the close of larval life, when the lungs come into use, the two hinder pair of arches disappear entirely * * * In the genus Spelerpes, which possesses a sling-like tongue, the lateral (dorsal) segment of the first true gill-arch grows out into a long cartilaginous filament which extends far back under the skin of the back." (Comparative Anat. of Vertebr., p. 74.)

In general, the hypobranchial apparatus of the 12 mm. larva corresponds very closely to the above description, but there are some minor points of difference. The hyoid is a single bar, the cerato-hyal, and shows no trace of a hypohyal, and the third and fourth branchial arches are not much smaller than the other two. The singular spatula-shaped urohyal is completely lost at the close of larval life. (See Plate 9.)

In Spelerpes, the protective capsule of the eye is not formed from the quadrate as in Rana, but by a slight process from the trabecular cartilages, and while in Rana (at 12 mm.), the auditory apparatus is merely a process arising from the trabeculae, in Spelerpes there

is a fully formed capsule. It is possible that the diverse habits of the two forms may account for this reversion of development. Spelerpes, which spends its larval existence for the most part hidden under rocks and in the dark, needs an acuteness of hearing and a sensitiveness to vibration for which its cousin compensates by an early developed and well protected eye.

TRABECULAE.—(Plate 10.) The trabeculae cranii appear as two longitudinal bars supporting the anterior end of the brain and the nasal sacs. Just behind the superior labial cartilages, they are flattened out into a pair of disk-like, slightly concave projections serving to support and protect the nasal sacs. There is no juncture of the trabecular bars here as is the case in the frog. Just behind the nasal capsule, the trabeculae resume their rod-like form, presently becoming compressed to form a sort of triangle, concave on the outside. This is the optic capsule before mentioned. Back of this point, the trabeculae are pierced by the optic foramena (Plate 8), and again, still further back, by another and larger foramen, which admits some of the larger vessels to the brain. Just above this latter foramen, the quadrate separates from the trabecula. This is given off from the upper half of the trabecular bar (Plate 8) and curves down to meet and articulate with the lower jaw (Meckel's cartilage), while the lower half curves in to meet its fellow just in front of the notochord (Plate 10, bp.), forming a support for the main part of the brain. The auditory capsule is continuous with the quadrate above and trabeculae below. From the point of their juncture, the trabecular bars continue as a pair of flattened rods—the parachordals (Plate 10), which together with the notochord form the floor of the brain case. Just behind the auditory capsule, the parachordals show a leaf-like process, which serves as a protective case for the medulla and upper cord.

UPPER LABIALS.—Plates 8, 9, 10, la.) These labials are a pair of rounded caps which fit over the ends of the trabeculae. They are pointed above and blunt below. It seems that these labials should be used, governed by suitable muscles, in sucking, in case the larva uses that means of obtaining food, but a diligent search failed to reveal any muscles which might be used in that way. The superior labials are, like the trabecular cartilages, entirely separate from one another. They are so freely and loosely articulated, moreover, as to permit of the possibility of considerable movement.

LOWER LABIALS.—(Plates 8, 9, lb.) The inferior labials, on the other hand, are so fused as to present the aspect of a single, compact cap, which fits over the rounded anterior part of the lower jaw. They are comparable in a general way, to the labials of Rana. The upper and lower labials are apparently among the first cartilages to appear, since at this stage they are very com-

pact and dense cartilaginous tissue, from which all trace of cartilage cells has disappeared.

MECKEL'S CARTILAGE —(Plates 8, 9, mc.) Meckel's Cartilage forms the basis and largest part of the lower jaw. It articulates in front with the bar of the lower labial, and fuses there, more or less completely, with its fellow of the opposite side. Behind, it articulates strongly with the quadrate (Plate 8, qd.). The cartilages are slender and rounded anteriorly, but become much heavier and more ovoid as they near their articulation with the quadrate. The coronary process is plainly marked, just in front of the posterior articulation, and directly under the optic foramen. The massive temporal and masseter muscles, which have their attachments on this process, together with the heavy pillar of the quadrate, form a bulging prominence which is readily discernible with the unaided eye.

THE QUADRATE.—(Plate 8, qd.). The quadrate is fused completely above with the trabecula, at a point dorsal to the second foramen, as before stated. Above and behind it fuses with the auditory capsule, while below it sends a heavy vertical bar to articulate with Meckel's cartilage. The quadrate is the heaviest solid cartilage in the skull at this period, and helps to form the rim of a deep protective socket within which the eyeball rests. The fusion of the quadrate with the capsule of the ear is only slight at this stage, but the mesoderm between the two parts is seen to be rapidly chondrifying, and indicates an extensive fusion later.

AUDITORY CAPSULE.—The auditory capsule, although not completely chondrified, can be traced very readily. The two capsules form the side wall of the skull, and indications of their juncture over the top of the brain can be detected. They are fused with the quadrates in front and with the trabeculae cranii below, but their posterior extremity is a free rounded surface. At the 12 mm. stage, therefore, the brain lies exposed above, but is protected laterally by the heavy auditory capsules and ventrally by the broad trabecular plate, and by the parachordals. The semicircular canals in the ear are fully formed, and there is full nervous connection with the brain. The circular (fibrous) patch so prominent in the frog at a similar stage can be detected, but with difficulty. It is the foreshadowing of the future stapes.

TEETH.—Teeth appear on the upper and lower labials and on both the trabeculae cranii and Meckel's cartilage. They are well along in development, and can be seen pushing their way through the skin of the mouth. They are beginning to appear on the branchial arches and ceratohyals as well.

BRANCHIAL APPARATUS.—(Plate 9.) The branchial apparatus of Spelerpes shows a marked difference from that of both Crytobranchus and Rana. The most noticeable features of the branchial cartilages of Spelerpes longicaudus are (*a*) the absence

of a basi-branchial plate, (*b*) the large size and peculiar contour of the urohyal, (*c*) the ceratohyals, which hang free from the basihyal, and do not articulate with the quadrate as they do in Rana and Cryptobranchus, and (*d*) the absence of any "free" branchials, that is, any branchials unattached to the basihyal cartilage.

BASIHYAL.—(Plates 8, 9, bh.) The basihyal is a rounded and slender rod of cartilage projecting well forward into the tongue and prolonged posteriorly into the slender urohyal. Just behind the rounded anterior extremity is found the articulation of the ceratohyals. This articulation is not close, but the ceratohyals seem to be rather loosely swung from the front of the basal cartilages. From the posterior portion of the cartilage, the first and second cerato-branchials are given off in close succession, and from this point the cartilage continues as the urohyal. In the specimen prepared, the basihyal and branchial cartilages were probably somewhat distorted, on account of the unnatural position of the tongue, so that in the drawing (Plate 8) they are higher in relation to the rest of the skull than they should be; the measurements, however, and relative sizes are accurate.

UROHYAL.—(Plate 9, uh.) The urohyal bar is much longer in Spelerpes longicaudus than in the same stage of the frog. It is median and basal, and forms simply an elongation of the basihyal. The urohyal terminates, however, in a flattened spatula, which affords a place of insertion for two heavy muscles.

CERATOHYALS.—(Plates 8, 9, ch.) The ceratohyals are a pair of curving bars of cartilage, swinging freely from a loose articulation with the anterior part of the basihyal. Their direction is dorso-caudal, and they terminate freely in the mesoderm a short distance behind the quadrate and external to the auditory capsule.

BRANCHIAL ARCHES.—(Plate 9.) The branchial cartilages at the given stage of this specimen are all in junction; that is, none of them hang free at either extremity. They may be classified into three pairs of ceratobranchials and four pairs of epibranchials.

The first ceratobranchial is the largest of all the branchial bars (Plate 9, bra.). It is given off from the anterior extremity of the basihyal. It curves slightly down and out and shortly gives rise to the first epibranchial and joins with the second ceratobranchial in originating the second epibranchial arch. The second ceratobranchials (Plate 9, brb.) are at their beginning noticeably smaller than the first ceratobranchials, but soon increase in size. This ceratobranchial gives rise to the second epibranchials (in conjunction with the first ceratobranchial bar) and to the third ceratobranchial (Plate 9, brc.). The third ceratobranchial soon divides into the third and fourth epibranchial cartilages (Plate 9, bc., bd.). The four epibranchials run free for some distance and at their posterior extremity are again united to one-another by a curving bar of cartilage.

MUSCULATURE.—A careful comparison of the muscles of this stage of Spelerpes longicaudus with the musculature of Rana and Cryptobranchus seems to show a close resemblance to Cryptobranchus, especially in the muscles of the branchial apparatus. Of course, no homologues of these muscles appear in the adult Rana, but even the larger head muscles correspond much more closely with those of Cryptobranchus. There appears to be no special modification for sucking, or any special muscles for that purpose. All of the muscles described are those of the adult Salamander in various stages of development. In the nomenclature of the muscles of the branchial apparatus, the analogies of Cryptobranchus have been very closely followed out.

MUSCLES OF THE HEAD.

M. TEMPORALIS.—(Plate 11, Fig. 1, mtm.) The temporalis is the most prominent of the muscles of the head. It arises on the quadrate cartilage, just posterior to the second foramen, and is inserted on the inner side of the coronary process. It is a broad, heavy sheet of fibres, broader at the insertion than at the origin. Its direction is ventral and slightly caudal. In reality, M. temporalis is made up of two parts, the one just described above, and a second, which I shall describe as—

M. PTERYGOIDEUS.—This is a thin strand of fibres arising on the quadrate bar, just below the origin of M. temporalis, and sending its fibres ventrally to unite with those of the temporalis. It corresponds very closely to the similar muscle in Cryptobranchus, which is described as follows; "This is a very insignificant muscle * * * and might almost be considered a fasciculus of M. temporalis. (Thesis, J. H. McGregor.) The muscle is entirely covered dorsally by M. temporalis, and acts with the temporalis in lifting the mandible, in opposition to the action of M. depressor maxillae inferioris.

M. MASSETER.—(Plate 11, Fig. 1, mm.) The masseter is a heavy, bulging muscle, partly covering M. temporalis. It arises on the anterior third of the auditory capsule, and, running downward and forward, is inserted on the outside of the mandibular bar (Meckel's cartilage), a short distance in front of the coronary process. The insertion of this muscle is comparatively very broad, though it is thick-bellied and rounded in the center.

M. DEPRESSOR MAXILLAE INFERIORIS.—(Plates 11, Fig. 1, mdm.). This is a large and powerful muscle, which, using the base of the lower mandible as a lever, depresses the jaws. It has two origins; the first in the middle of the optic capsule, just posterior to the origin of M. masseter, and a second, which is lower and posterior to the first. The fibres from the two origins, however, soon intermingle, and evidence of the double origination is lost. The muscle extends down and forward, parallel to

M. masseter, and is inserted on the rounded base of the lower mandible (Meckel's cartilage). Turning now to the ventral surface, we find the—

M. SUBMAXILLARIS.—(Plate 11, Fig. 2, msb.) This muscle is a broad, thin sheet of fibres covering in the space between the mandibles almost completely. It extends between the two rami throughout their extent, save for a small space at their anterior extremity. The muscle is a very delicate one, and the fibres are loosely conjoined, seeming to indicate a tardy development as compared with the other muscles. The function of the submaxillaris is still a matter of doubt, but that it is closely connected with the respiratory function seems fairly certain.

M. SUBMENTALIS.—(Plate 11, Fig. 2, msm.). This small and insignificant muscle appears as a tendinous band at the extreme anterior portion of lower jaw. Its function is to approximate the rami of the jaw, but it appears to be of small practical consequence.

MUSCLES OF THE BRANCHIAL APPARATUS.

The branchial muscles of the 12 mm. Spelerpes longicaudus show a very marked similarity to those of the adult Cryptobranchus, although they are not quite so numerous, or so complex. The group consists of a paired sternohyoid, a hypobranchial, a constrictor, levator and depressor of the arches, a geniohyoid, a well defined cerato-branchialis and a small omohyoideus.

M. STERNO-HYOIDEUS.—(Plate 11, Figs. 2, 3, msh.) This muscle is a direct continuation of the fibres of M. rectus abdominis. The recti abdomini, as they pass forward from the posterior part of the body, alter both in contour and in position. In the body proper, they are seen as two thin vertical sheets of muscle, bounding the body cavity. As they pass into the head region, however, they gradually assume a median position and become thickened to form a pair of round, heavy muscles, which fuse in the region of M. temporalis, and have their common insertion on the basihyal at the point of union of the first ceratobranchial. The muscle is superimposed on the urohyal cartilage.

M. GENIOHYOIDEUS.—(Plate 11, Figs. 2, 3, mgh.) This muscle arises on the lower mandible, just posterior to the insertion of M. submentalis. From this point it extends directly backward, as a small rope-like muscle, to its insertion on the spatular end plate of the urohyal cartilage. Its function is to draw the branchial apparatus forward.

M. HYPOBRANCHIALIS.—(Plate 11, Fig. 3, mhb.) This muscle arises on the ventral surface of the ceratohyal cartilage, inside of the origin of the following muscle. Its fibres run posteriorly and obliquely inward, and are inserted along the course of the posterior two-thirds of the first epibranchial, except at the posterior end of the branchial.

M. CERATOBRANCHIALIS.—(Plate 11, Fig. 3, mcb.) This muscle is a thin sheet of fibres arising on the ventral surface of

the ceratohyal cartilage, just outside of the origin of M. hypobranchialis, and sending its fibres inward to the extremity of the operculum. The function of the muscle is to raise the opercular fold and to create thus a suction through the gill slits. There is, of course, no homologue of this muscle either in Rana or in Cryptobranchus.

M. LEVATOR ARCUUM BRANCHIALIUM.—(Plate 11, Fig. 1, mla.) This slender and insignificant muscle arises as a fasciculus of M. longissimus dorsi. It is given off from that muscle at the extreme posterior end of the otic capsule and extends posteriorly and obliquely downward to an insertion on the first epibranchial bar. It serves to raise the branchial apparatus.

M. CONSTRICTOR ARCUUM BRANCHIALIUM.—Plate 11, Fig. 3, mca., mce., mci.) This muscle is divided into three equal parts, which, from a common origin, separate and run to three distinct and different insertions. The muscle itself is a continuation or prolongation of the fibres of M. hypobranchialis, and takes its course along the inner or body side of the arches. Its first fasciculus is inserted on the course of the second epibranchial cartilage, its second fasciculus on the the third epibranchia and its third part along the course of the last arch. Its evident function is the closing of the branchial clefts, acting with M. ceratobranchialis to create a suction of water through the clefts.

M. DEPRESSOR ARCUUM BRANCHIALIUM.—(Plate 11, Fig. 2, mdb.; Fig. 3, mab.) This muscle is a sheet of fibres arising on the inner side of the last branchia and sending its fibres inward to mingle in the middle line. The main part of the muscle is just anterior to the tracheal opening, and some of its fibres even mingle with those of the following muscle. The name of the muscle indicates its function.

M. OMOHYOIDEUS.—This is a rather small and insignificant muscle at this stage. It arises in the region of the future scapula and sends its fibres downward to mingle around the trachea. This muscle does not function before the metamorphosis, and as no sign of a scapula appears, it cannot now be traced to a definite origin.

BODY MUSCLES.

The two body muscles which appear at the present stage are the M. longissimus dorsi, and M. rectus abdominis.

M. LONGISSIMUS DORSI.—(Plate 11, Fig. 1, mld., mli.) This large and important muscle has a double origin. The first is on the auditory capsule, on the dorsal side next to the surface, and in the region of the articulation of the jaw and of the eighth nerve. The second origin is considerably posterior to the first and is at the base of the brain, on the parachordal cartilages. From their origins, both fasciculi run directly tailwards, uniting in the region of the tenth nerve, to form a dumb-bell shaped muscle which partially surrounds the medulla. After this point, the muscle rapidly increases in size, as it runs on back toward the tail.

M. Rectus Abdominis.—(Plate 11, Fig. 1, mra.) The sternohyoideus muscle, already described, is a continuation of M. rectus abdominis. As the muscle runs back, it becomes more and more flattened, until it presents the typical aspect of a thin sheet of tissue lining the ventral body wall. In this specimen it presents no unusual characteristics.

MUSCLES OF THE EYE.

No well defined musculature for the eye was found, but two recti muscles, or traces of them, could be distinguished. They are very small, and while their insertion on the eyeball can be seen plainly, their origin is lost in the surrounding mesoderm.

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Volume VI, page 45—"Preliminary Notes on the Cranial Nerves of Cryptobranchus allegheniensis."—*J. H. McGregor.*

Volume VI, page 54—"On Three Points in the Nervous Anatomy of Amphibia."—*J. S. Kingsley.*

Volume VII, page 146—"Preliminary Notice upon the Cytology of the Brains of some Amphibians."—*S. E. Jelliffe.*

Volume VIII, page 314—"On the Weight and Length of the Central Nervous System in Bull-frogs of different Sizes."—*H. H. Donaldson.*

Volume IX, page 53—"Nerve Termini in the Skin of the Common Frog."—*G. E. Coghill.*

American Naturalist—Volume XXXIII, page 231—"Desmognathous fusca and Spelerpes bilineatus.—*Harris H. Wilder*

Thesis, Ohio State University—"Osteology and Myology of Cryptobranchus allegheniensis."—*J. H. McGregor.* (Unpublished.)

Journal of Morphology—

Volume II, page 297—"On the Relations of the Hyoid and Otic Elements of the Skeleton in the Batrachia."—*E. D. Cope.*

Volume VII, page 189—"The Development of the Optic Vesicles in Amphibia."—*A. C. Eycleshymer.*

Volume VII, page 23—"Studies on the Development of the Ear in Amblystoma."—*H. W. Norris.*

Volume X, page 101—"The Cranial Nerves of Amphibia."—*O. S. Strong.*

Volume X, page 231—"The Central Nervous System of Desmognathous fusca."—*Pierre A. Fish.*

"The Frog."—*Ecker.*

"Vertebrate Embryology."—*Marshall.*

"Manual of Vertebrates."—*Jordan.*

Journal of the Philadelphia Academy—Volume I, page 287.—*Baird.* Volume IV, page 345.—*Hallowell.*

Proceedings Academy Philadelphia. 1869—Page 107.—*Cope.*

"Salamandridae," page 82—*Strauch.*

"Batrachia of North America."—*Cope.*

EXPLANATION OF PLATES.

KEY TO PLATE 8.

A reconstruction of the skeletal elements of the head.

SIDE VIEW

la.	Upper labials.	pc.	Parachordal cartilages.
tr.	Trabecula.	pf.	Posterior foramen.
lb.	Lower labials.	pn.	Coronoid process.
qd.	Quadrate cartilage.	au.	Auditory capsule.
mc.	Meckel's cartilage.	ba.	First branchial arch.
bh.	Basihyal cartilage.	bb.	Second branchial arch.
ch.	Ceratohyal cartilage.	bc.	Third branchial arch.
nb.	Nasal capsule.	bd.	Fourth branchial arch.
op.	Optic foramen.		

KEY TO PLATE 9.

A reconstruction of the skeletal elements of the head.

VIEW OF THE BRANCHIAL APPARATUS.

bh.	Basihyal cartilage.	ba.	First epibranchial cartilage.
uh.	Urohyal cartilage.	bb.	Second epibranchial cartilage.
bra.	First ceratobranchial cartilage.	bc.	Third epibranchial cartilage.
brb.	Second " "	bd.	Fourth epibranchial cartilage.
brc.	Third " "	ch.	Ceratohyal cartilage.

KEY TO PLATE 10.

A reconstruction of the skeletal elements of the head.

VIEWED FROM ABOVE.

tr.	Trabeculae.	pc.	Parachordal cartilages.
bp.	Basal plate of the trabeculae.	au.	Auditory capsule.
la.	Upper labials.	ch.	Notochord.
nb.	Nasal process.		

KEY TO PLATE 11.

Reconstruction of muscles.

Figure 1.—Lateral view

Mtm.	M. temporalis.	Mra.	M. rectus abdominis.
Mla.	M. levator arcuum branchialium.	Mcb.	M. cerato-branchialis.
Mld.	M. longissimus dorsi.	Mdm.	M. depressor maxillae inferioris.
Mli.	M. longissimus dorsi, inferior fasciculus.	Mm.	M. masseter.

Figure 2.—Ventral view.

Msm.	M. submentalis.	Mdb.	M. depressor arcuum branchialium.
Msb.	M. submaxillaris.		
Mcb.	M. cerato-brenchialis.	Mgh.	M. genio-hyoideus.
Msh.	M. sternohyoideus.		

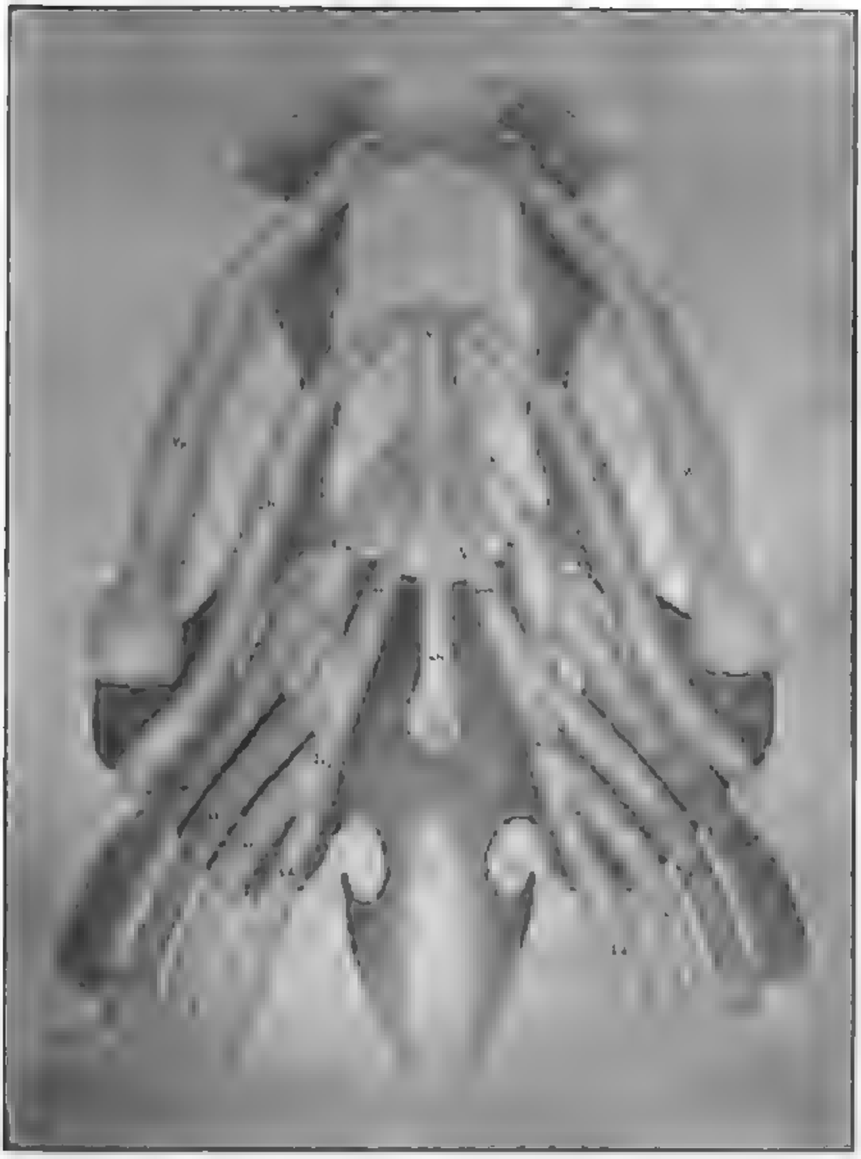
Figure 3.

Reconstruction of branchial musculature.

Msm.	M. submentalis.	Msh.	M. sternohyoideus.
Mgh.	M. geniohyoideus.	Mca.	M. constrictor arcuum branchialium, first fasciculus.
Msb.	M. submaxillaris.		
Mcb.	M. cerato-branchialis.	Mce.	M. constrictor arcuum branchialium, 2nd fasciculus.
Mhb.	M. hypobranchialis.		
Mab.	M. depressor arcuum branchialium.	Mci.	M. constrictor arcuum branchialium, third fasciculus.

In the reconstruction, the ceratobranchial muscles are removed, the sternohyoideus muscles are cut out so as to show the M depressor arc-branchialium, and one of the geniohyoideus muscles has been cut to show the origin of M sternohyoideus. The submaxillaris has been represented as slit, and the flaps turned back.

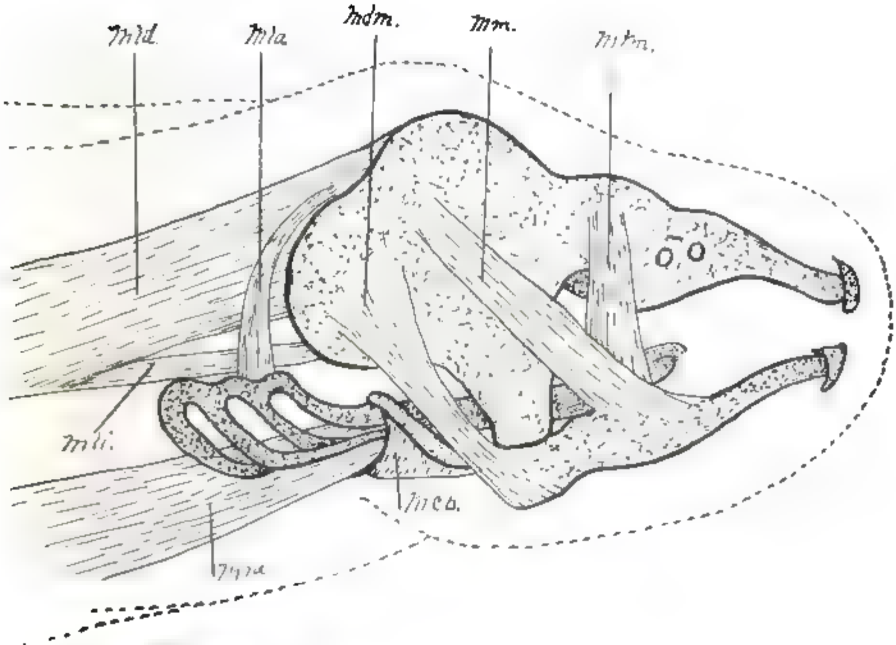
HOUGHTON on "Spelerpes longicaudus."



HOUGHTON on "Spelerpes longicaudus."

Houghton on "Spelerpes longicaudus."

Fig. 1.



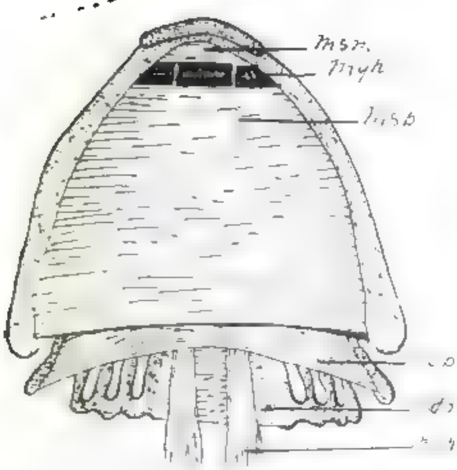


Fig. 2.

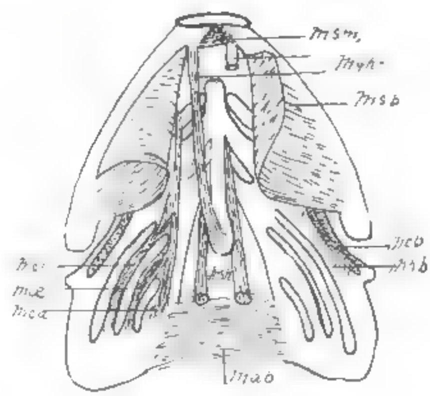


Fig 3.

HOUGHTON on "Spelerpes longicaudus"

ON THE AUTUMNAL SONGSEASON.*

J. R. TAYLOR.

What I have to say is so patently unscientific that my first word must be a disclaimer of any such intention. Subjective method like mine is, I know, anathema in science. From an objective standpoint there is no music in the Brown Creeper's note; it is a creaking, a filing, an old chair is as musical; yet I have followed it as Ferdinand followed Ariel. It is courage come to share our winter, a conclusion not necessarily unscientific. Imagination, witness the discovery of Neptune or the setting up of the mastodon from fragments of bones, is as great a force in science as in the arts; and there is no great gulf fixed between science and art, the mind working not differently in the two fields. We of the opposite camp follow beauty, you truth; the Cardinal in the snow means as much by one method as by the other. Therefore if we learn gladly of the scientists, the reverse is true also; and because I have learned birds chiefly by their songs, I find I have to ornithologists, and however small it may be, interesting and supplementary information.

Even scientists know that there is a definite songseason, in a way synchronous with the breeding season, from March to June. It is also well known that birds sing beyond this period, the only absolute lulls seeming to fall in August and in December. I have heard the Bluebirds singing in the snow at Christmas, the Robin on New Year's Day; and the Carolina Wren, in the words of Mr. Riley, sings when he durn pleases. But the spring songseason remains fixed and unapproachable for its continuity and multitude of song. What has been more neglected is the autumnal songseason, which seems to me also a definite period, more or less immediately preceding the departure of the birds for the south. At the end of August, this summer, the Orioles and the Warbling Vireos, after many weeks of silence, were all singing again on the campus, and soon after, of course, were gone. This, I think, is a habit which may be found to be universal. I cannot be sure of certain birds. The Whippoorwills sing on into September apparently without a break. In the Adirondacks a few years ago the Barred and the Great Horned Owls were silent in July and August, and hallooed over the lakes all night long in September; but in their case this could hardly precede a migration. I have heard the Bobolinks sing for a few moments in the dawn, at the end of August, after they must have changed plumage, and after more than a month of silence; I have heard the Red-winged Blackbirds in October in a chorus unheard since early July; and the list might be made a long one, in each case preceded by a

*Read before the Wheaton Club of the Ohio State University, October 14, 1901

long interval of silence, and heard at a certain date year after year. Not to mention the singing migrants, varying widely from the Upland Plover to the Whitethroats, Solitary Vireos, Ruby-crowned Kinglets, the following will serve as examples. Both the Orioles sing in late August and early September; Field Sparrows in September, Vesper Sparrows into October, Fox Sparrows into November; the Warbling and the Red-eyed Vireos in September; the Maryland Yellowthroat in September, and in the same month the Catbird and the Brown Thrasher; and more rarely I have heard the Woodthrush also, though he sang only the preludes without the flute-notes. I have never heard the Flycatchers sing again after their summer silence, nor the Tanagers, nor the Martins, nor many of the Warblers and Thrushes.

In each case, the song seems an accompaniment or precursor of migration. The Junco's addition to his song, in April just before he departs for the north, is parallel. I cannot presume to offer an explanation. To me it seems several possible things; memory of the spring's journey bringing a repetition of the song; or rehearsal and education of the young birds, although it seems to me difficult to prove that only the young birds sing; or, as it has been called, "false dawn" of sex, a mating without the nesting, which I have seen the Mourning Doves do; or, perhaps fantastically, farewell to the land of the nests of northern summer. If it is true that the Grouse will drum on the old courting log even in October, a recognizably sentimental operation, none of the suggestions is preposterous. Why birds sing is hardly to be explained by anatomy. The general opinion of ornithologists seems to be that song is an expression of pleasure, and that birds do not sing in fear or sorrow. I have known a particularly gorgeous sunset to waken the Woodthrushes in midsummer, and it seemed to me not unlikely that the pleasure of the rich color sensation might partly account for it. It is probable that the autumnal songseason is a time of gayety and novelty, a recognition of old places, an anticipation of new, together with some associated memory of the choosing of the mates. The impression may be further explained by the character of the song in autumn.

It is always difficult to hear and know the autumnal songseason, both because it is so much less in volume and continuity than in spring, and because it is not like that of April full-throated. The quality is changed,—if I were before a less formidable audience, I should say sea-changed. For it is as if the birds were singing under water, underground. It is as if they sing without opening their beaks; which indeed they seem sometimes to do even in spring, for I have heard both the male and the female Thrasher sing so in the nesting, each with the twig or straw in mouth; and I have never heard the Hermit Thrush in spring migration sing in any other way. This last instance may

illustrate my meaning. I have verified the experience through several Aprils. The first hearing was in this manner. For a long time I had been sitting still to watch the Hermit flitting and returning among the naked copses by the old river-bed; and what with his nearness and the fresh April song about me, the memory of his song came to me clear and clearer. Let not Science reproach me for this!—I was fancying what old law, what jealous traveler's silence on the way to the happier north his home, kept unuttered in the bird's white breast that high romance, the voice of our best dreamer, even the memory of which made sunset flash across the mountain lakes to me. The memory, the fancy, grew so vividly upon me that I smiled to find myself placing actually somewhere, across the Olentangy, upstream, downstream, the phantom singing of my own creation. Then I woke to the realization that it was an actual song, a Hermit Thrush really singing, but very far away. And last of all, I saw the dappled throat of my Thrush, which was always here and there about the leafless thickets, near me in the sun, saw his throat ruffling, and knew that he was the singer of the song that seemed, across the river or across the years, so far away.

I ask pardon for such unedifying rhapsody, but the quality thus suggested is characteristic of the autumnal songseason. Some birds apparently change the form as well as the quality of their song, making of it an entirely new composition; the Bob-white, for instance, and (I think) the Chickadee; and the Carolina Wren in September has often set me hunting down a new song, surprising me at length to find him, that piper of indomitable and far-ringing cheerfulness, now singing a secret bubbling continuous Goldfinch-like song. But most of our birds, without changing the form of their song, change the tone-color as I have described. So the Catbird sings, so the Brown Thrush; at your shoulder, may be, but seeming a half mile away; so sing our most frequent autumnal vocalists, the Meadowlarks, Cardinals, Song-sparrows, Robins; half-song, a whisper-song, an echo, a ventriloquism. It is, I suppose, simply that they sing with half-voice, as we might hum to ourselves a melody that haunts us through the day's work.

But it is easier for me to deal with effects than with causes, and I shall not this time apologize, for these are my last words. The autumnal song seems to me not less beautiful than that of April; not the same triumphant, but memorial, charged with emotion, an art wrecked by its own beautiful joy; autumn's fit utterance, when even Anosia, the red monarch of all the butterflies, migrates among the departing birds and the unreturning leaves; and when always across the sky, in October, in November, as long as the Witch-Hazel is in flower, the Bluebirds play their pipes of passage.

FOOD PLANTS OF SOME BYTHOSCOPIDAE.

E. D. BALL, Utah Ag. College, Logan, Utah.

In giving food plant records it seems desirable to distinguish those records that are the result of repeated observation, or made under circumstances that admit of slight chance for error, from those that are based on accidental occurrence of one or more specimens upon some given plant. The adults of most all of our leaf-hoppers fly very readily and are often found on plants adjacent to the one they feed upon, especially after a sweep net has been vigorously used in the neighborhood. And too often there is no means of knowing whether the record is the result of one accidental specimen or the summation of a life-history study.

The longer the author studies the food plant relations of the Jassidae the more evidence he finds to support the idea that nearly every species has its particular food plant or group of closely related plants upon which it is almost absolutely dependent in part, at least, of its life cycle. In a large number of species the larvae rarely if ever leave the plant upon which they emerge from the eggs. So that the finding of the larvae in any number upon a plant is in a great many cases an almost absolute test of the correctness of the food plant determination.

The following notes are in many cases extracts from almost complete life-history studies and in every case are based on sufficient evidence to almost preclude the idea of an accidental occurrence.

GENUS MACROPSIS.

The following notes complete the food plant list for our forms of this genus, with the exception of one species, and while the genus as a whole presents a remarkable variety of food plants each species seems to be very strictly confined to its particular plant or group of closely related forms. In fact I have even found the presence of a particular species of Macropsis one of the best guides to the determination of the many varieties of one plant species.

M. laeta Uhl.—This species is found only on the bushy species of Sumac (*Rhus aromatica* and *trilobata*), that occur so commonly on the sides of the foot hills and along the bluffs of the streams out on the plains in Colorado. The larvae appear early in July, hiding in the axils of the leaves and in the fruit clusters. They mature early in August, the adults remaining until the middle of September. They are of a bright, shining green color and thus resemble the petioles and new growth upon which they stay.

Var. *paeta* Ball.—Is a pink variety of this species found only in the crimson fruit clusters of this Sumac, where it is well protected

by its resemblance to the fruit stems and also by the sticky nature of the fruit.

M. humilis Stal.—This species seems to be strictly confined to the rayless golden rod (*Bigelovia douglasii* group). The female is of a pale green color, similar to that of the new growth upon which it stays. The male has a shining black stripe down the back and depends upon its agility in dodging around the stems for protection. The adults appear in July, the males having mostly disappeared by August 1st. It is a common species in southwestern Colorado and occurs sparingly well up in the mountains west of Fort Collins, Colo., but has never been taken in the foot hills or on the plains, although the Bigelovia abounds there.

M. robusta Uhl.—This small pale green form is found abundantly on the bushy Atriplex (*A. canescens*) throughout the southern half of Colorado and down into Arizona. The plant appears almost white, but the young shoots and stems where the insects rest are pale green.

M. bisignata Ball.—This pretty brown-marked species occurs on *Gutierrezia euthamiae*, a little yellow-flowered Compositae that grows in small clumps all over the plain region of Colorado and well up into the mountains. There appears to be two broods of this species, one appearing late in May and another in September. The difference in altitude affects the time of appearance so much that it is hard to determine the number of broods except where the same locality is under observation during the entire year.

GENUS PEDIOPSIS.

The food plants of a number of our species have already been definitely recorded and a few more are added here. The willow forms, as far as studied, seem to be as strictly confined to one species or group of willows as are the willow-inhabiting forms of Idiocerus.

P. tristis Van D., and *trimaculata* Fitch.—were both injuriously abundant on cultivated plums at Fort Collins, Colo., in 1902. The adults of the latter species appeared the first week in July and those of *tristis* a week or more later.

P. suturalis O. and B.—seems to be strictly confined to the black willows (*Salix amygdaloides* and *nigra*), where it is fairly common locally.

P. erythrocephala G. and B.—An abundant species on the narrow-leaved willow (*S. longifolia*). By an oversight the habitat of this species was omitted in Osb. and Ball's review of this genus. It is known from Iowa, Nebraska, Kansas and Colorado.

P. trivialis Ball.—This species occurs abundantly on the black willows (*S. amygdaloides*) in Colorado. The adults appear by the first of July.

P. viridis Fitch.—This species appears to be strictly confined to the narrow-leaved willow (*S. longifolia*). The adults appear the middle of June.

GENUS IDIOCERUS.

The American forms of this group have been recorded from only three genera of plants and these all tree forms. The following notes add as many more genera to the list and introduces for the first time strictly bush forms as host plants. Wherever willow forms have been studied they have been found confined to one species or to a group of closely related species of willows and not general feeders as has been commonly supposed.

I. dolosus Ball.—Found only on the bushy Sumac (*Rhus aromatica*) in the mountain region of Colorado. Adults have been taken from the middle of July until late in August.

I. ramentosus Uhl.—Common on *Salix longifolia*, seeming to prefer the short, thick clumps and sheltered locations. Found in Iowa, Nebraska and Colorado.

I. snowi G. and B.—found on *S. longifolia*.

I. lachrymalis Fitch.—found only on the Quaking Asp (*Populus tremuloides*).

I. femoratus Ball.—is a willow form, but has not been found in sufficient numbers to determine which species of willow it lives on.

I. productus G. and B.—is also a willow form.

I. morosus Ball.—This was swept commonly from two species of *Ribes* growing in the foot hills and mountains west of Fort Collins, Colo. It was most frequently met with on the red currant or squaw berry (*R. cereum.*)

I. verrucosus Ball.—was also taken on currants at about the highest altitude at which they grow.

I. ensiger Ball.—This is probably another currant form, though not enough specimens were taken at any one time to eliminate the possibility of it being an accidental capture. There were two very distinct kinds of larvae found together on the squaw berry—one, dark reddish brown that apparently belonged to this species, and a green form that was probably *morosus*.

I. amoenus Van D.—This pretty species lives on the Juniper, where its rufous and green match well with its surroundings.

I. nervatus Van D.—This species has been reported as occurring on willows, but in Colorado it seems to be an inhabitant of the Juniper. It is possible that there are still two species mixed under that name.

The American Association.

We have been interested in noticing the membership of the American Association for the Advancement of Science from the different Universities of the country, as shown by a Geographical list recently published by the Association.

In this list the Institution is given, although possibly not stated in all cases, but on the basis of this list and adding such as are known to belong to the University staff in each case, the numbers run as follows:

Columbia, 52; Cornell, 34; Ohio State University, 28; Harvard, 27; Chicago, 24; Yale, 23; Johns Hopkins, 18; Stanford, 17; Wisconsin, 16; Michigan, 15; Minnesota, 15; Indiana, 14; Syracuse, 13; Illinois, 12; Kansas, 12; California, 12; Princeton, 12; Nebraska, 11; Missouri, 10; Iowa, 8; West Virginia, 8; Western Reserve, 8; Case School, 8; Texas, 7; North Carolina, 7; Colorado, 6; Washington at St. Louis, 6; Maine, 5; Tennessee, 5; Vanderbilt, 5; Oberlin, 5; Purdue, 3; Virginia, 3; Cincinnati, 1.

We note the following for Ohio cities. Cleveland, 41; Columbus, 37; Cincinnati, 21; Oberlin, 6; Wooster, 6; Marietta, 5; Akron, 4; Westerville, Delaware, Athens, Alliance, 3 each; Ashtabula, Covington, Hiram, Painesville, Springfield, Tiffin, Toledo, Wilmington, Youngstown, 2 each; Barnesville, Dayton, Defiance, Elyria, Fredericktown, Garrettsville, Gilmore, Granville, Greenville, Hamilton, Mt. Vernon, New Carlisle, North Baltimore, Oxford, Plainville, Rushsylvania, Salem, Sandusky, Signal, Urbana, Warren, West Milton, Wheelersburg, Wyoming and Zanesville, 1 each.

OHIO MYCOLOGICAL CLUB.

To the Botanical Department came ever more frequent inquiries as to the mushrooms and toadstools and other of the higher fungi. It was thought best to devise a plan of response that would be less burdensome and at the same time a better means of furnishing, as far as could be done, the information sought, and perhaps render assistance to people not now nor intending to be students in colleges.

Accordingly it was decided to form a Mycological Club, unencumbered by constitution, by-laws, or officers, open to everybody, and with the sole object of mutual help in observing and studying the numerous mushrooms and toadstools—learning them so thoroughly that the different kinds, especially the commoner species, could be accurately identified with a view of using the edible and avoiding the poisonous kinds. It was determined to fix the fee at ten cents—low so as not to be burdensome to anyone—and strong hope was entertained that with the income so obtained several bulletins could be issued during the season.

All who were consulted permitted their names to be entered as charter members, and the Ohio Mycological Bulletin, No. 1, was issued. The members now number over 200 and the membership cards are still being received. It is interesting to observe that

the list includes school pupils, college students, many amateurs, professional botanists (among these several eminent American Mycologists,) business and professional people—not confined to Ohio but from the whole country.

The first four-page bulletin gave a few introductory and explanatory paragraphs, nine figures illustrating the general appearance of the commoner groups of mushrooms, namely, the Gill-fungi, Pore-fungi, Spine-fungi, Coral-fungi, Carrion-fungi, Puffballs, Earthstars, Cup fungi, and Morels. Three illustrated books noticed, suggestions to teachers, a paragraph on the Gill-fungi, and the list of seventy-six charter members are the other contents of the first number.

Bulletin No. 2 has just appeared. Besides explaing the make-up of a botanical name, giving directions for sending specimens, and the second list of members, the Morels are discussed and illustrated by two full-page plates, showing the plants natural size.

All the botanical names and the uncommon descriptive words used in the bulletin are divided into syllables, and the accented syllables marked. All matters are made as clear as possible. All who may be interested in the mushrooms or who desire the bulletin are invited to join the club, sending their names with fee to the Professor of Botany, O. S. U., Columbus, O. —O. M. B.

Meeting of the Wheaton Club.

The Club met Monday evening, March the 16th, in Biological Hall. After a short business session the Club proceeded to an examination and discussion of the list of earliest spring migrations for Columbus, published in the February NATURALIST. Comparison with the migration dates of Dr. Wheaton showed in most cases a close connection, although there were several records differing quite widely. The record of the kingbird, *Tyrannus tyrannus*, was found to be based on a mistake in the records of the Club. Discussion brought out the fact that several of the dates given were antedated by observations of the members which had not been reported and were therefore not available when the list was made up. The new records are given below:

Barn Swallow, April 14.	Whip-poor-will, April 29.
Rose-breasted Grosbeak, April 22.	Kentucky Warbler, April 30.
Orange crowned Warbler, April 22.	Great crested Flycatcher, April 29.
Maryland Yellow-throat, April 20.	Black-billed Cuckoo, May 5.
Rough-winged Swallow, April 24.	Blue-headed Vireo, April 30
Olive-backed Thrush, April 26.	Prothonotory Warbler, April 28.
Warbling Vireo, April 20.	Yellow-billed Cuckoo, April 27.

After the discussion, reports of personal observations were made, Mr. Dawson reporting the Goshawk for March 15th. The Club then adjourned to meet April 20th.

WALTER J. DERBY, *Secretary.*

MEETING OF THE BIOLOGICAL CLUB.

ORTON HALL, February 2, 1903.

The first paper was given by Prof. Dresbach, on "Some Peculiar Variations in Blood Corpuscles." He reported finding a person whose blood corpuscles are elliptical. Their dimensions are as follows:

Greatest width, 4.8μ. Greatest length, 10.3μ.
Average width, 4.1μ. Average length, 10.μ.
Average thickness through center, 1.3μ.
Average thickness through edge, 2.7μ.
Ratio of width to length, from 1:2 to 1:3.1.
The average human corpuscle is 7.2μ to 7.8μ in diameter.

The scond paper of the evening consisted of a review of the life of Pasteur, by Mr. Landacre. After dealing with the main facts of his life, especial emphasis was laid on two phases of it; first, the directness of his method in research. Almost every great discovery Pasteur made was first undertaken as the result of influences brought to bear on him by others. The reasons for beginning researches with him were usually economic. His life seems to be a refutation of the current belief that the best scientific work can be done by allowing each man to follow his own inclination. Second, there was a remarkable sequence in his researches. Each one grew out of the preceding problem. And yet it was always the practical side of a problem that attracted his attention.

Under personal observations, Dr. Kellerman spoke of the abundance of *Chaerophyllum procumbens* along the Olentangy. He noticed that almost every plant was very badly infected with a black rust. They have a red rust in spring and later a black rust, but it is unusual to find them infected in winter. He also spoke of his inoculation experiments with rusts and gave a summary of his paper, which is published as a University Bulletin, Series 7, No. 11. (Botanical Series, No. 12.)

Mr. Mead reported on the examination of the flora of a mound near Chillicothe. It had been reported that there were some peculiar plants growing near it. His investigations, which included the determination of the whole flora, showed, however, that there were no plants present the occurrence of which was at all unusual.

Prof. Schaffner exhibited some mangrove embryos from Florida and remarked upon the habits of the plant.

Prof. Osborn gave a note on a report concerning the campaign against mosquitoes on Long Island. This is published on p. 377 of the February number of THE NATURALIST.

ROBERT F. GRIGGS, *Secretary*

8

Columella Auris and Nervus Facialis in the Urodela.

By B. F. KINGSBURY.

[Reprinted from THE JOURNAL OF COMPARATIVE NEUROLOGY, Vol. XIII, No. 4, December, 1903.]

COLUMELLA AURIS AND NERVUS FACIALIS IN THE URODELA.[1]

By B. F. Kingsbury.

The following communication sets forth the results of a study made upon the relations and development of the parts in the otic region of the head in Necturus maculatus, and in comparison with that form, Desmognathus fusca and Spelerpes bilineatus.

The need for a careful study of (1) the relations of the facial nerve to the columella auris in the various Urodela, and (2) the homology of the suspensorio-opercular connections in the different forms of Amphibia has been emphasized by Gaupp.[2] From a comparison of the statements of Wiedersheim,[3] Huxley,[4] Parker,[5] and Hasse[6] he was lead to conclude

[1] This may be considered as a partial preliminary communication upon the development of the skull of Necturus maculatus, undertaken at the suggestion of Professors Wiedersheim and Gaupp, in the Anatomisches Institut at Freiburg. I wish to acknowledge my indebtedness to them and to Professor Keibel and others, for suggestions and material. Since the completion of this manuscript in May 1902, more than a year has elapsed, and in sending it to the press now, I take the opportunity of noticing papers that have appeared in the meantime—those of Kingsley and Coghill.

[2] '98, Gaupp, E. Ontogenese und Phylogenese des Schalleitenden Apparates bei den Wirbeltieren. *Merkel u. Bonnet, Ergebnisse d. Anat. u. Entw.*, 1898, Bd. VIII, pp. 989–1149.

[3] '77, Wiedersheim, R. Das Kopfskelet der Urodelen. *Morph. Jahrb.*, Bd. III, pp. 352-548.

[4] '74, Huxley, Th. H. On the Structure of the Skull and the Heart of Menobranchus lateralis. *Proc. Zool. Soc.*, 1874.

[5] '77, Parker, W. K. On the Structure and Development of the Skull in the Urodelous Amphibia. Pt. I. *Philos. Trans. Roy. Soc.*, Vol. 167, Pt. 2.

'82a, On the Morphology of the Skull in the Amphibia Urodela. *Trans. Linn. Soc.*, Ser. 2, Vol. II.

'82b, On the Structure and Development of the Skull in the Urodeles. *Trans. Zool. Soc.*, London, Vol. XI, pp. 171-214.

[6] '73, Hasse, C. Ueber den Bau des Gehörorgans von Siredon pisciformis und über die vergleichende Anatomie des Kiefersuspensorium. *Anat. Stud.*, Bd. I, No. XV.

that there were apparently two methods of connection of the operculum with the suspensorium (quadratum). Thus, WIEDERSHEIM gives as the universal condition, that the nervus facialis passes *above* the suspensorio-opercular connection; HUXLEY described a suspensorio-stapedial (opercular) ligament *under* the facial nerve; HASSE, in Siredon (Amblystoma) described the nerve as under the columella; while the statements of PARKER are not always clear, though it is evident that in the different Urodela both relations of columella or suspensorio-opercular ligament and nerve were described.

The study of the relations in the three forms above mentioned, to which Proteus anguineus, Amphiuma means, and Amblystoma tigrinum (larva) may be added, has shown that in all except Necturus, the nervus facialis passes below (ventrad to or cephalad of) the suspensorio-opercular connection. In Necturus, the ramus jugularis facialis passes above (dorsad to) the ligament, the remainder of the nerve, i. e. ramus mandibularis externus and internus, and ramus palatinus being below (ventrad or cephalad to) this structure. Furthermore, in these three forms, the columella or ligament passes from the operculum to the bone which lies partly upon the ear capsule and partly upon the external surface of the quadratum—and which, as far as I can judge from the evidence at hand, I regard as a squamosum;—and not (primarily) to the cartilage of the quadratum as heretofore stated. This is a fact of considerable morphological importance. A more detailed description of the relations in the forms follows:

Necturus Maculatus. In this form HUXLEY[1] described the "suspensorio-stapedial ligament" as arising from the "middle of the posterior edge of the quadratum—and passing upwards and backwards to the stapes. The Hyomandibular branch of the seventh nerve passes passes above this ligament to its distribution just as it passes above the columella auris in the Frog." WIEDERSHEIM made no different statement of relations. This structure described by HUXLEY, which was presumably a sheet of

[1] Op. cit. p. 192.

fascia, is not the true suspensorio-opercular connection, which is correctly described by COPE,[1] as passing from the operculum to

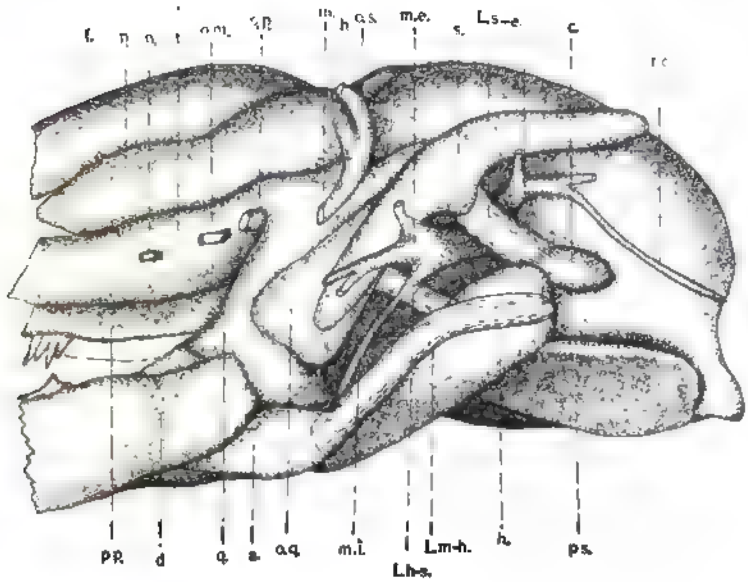


Fig. 1. Diagram from a drawing of the left side of a model of the skull of a Necturus 49.5 mm. long.

a.—Os articulare (angulare ?). *b.*—Nervus buccalis.
c.—Columella (operculum). *d.*—Os dentare.
f.—Os frontale. *h.*—Ceratohyale.
j.—Ramus jugularis VII
L. h.-s.—Ligamentum hyo-suspensoriale.
L. m.-h.—Ligamentum mandibulo-hyoidale.
L. s.-c.—Ligamentum squamoso-columellare
m. e. VII.—Ramus mandibularis externus facialis.
m. V.—Nervus maxillo-mandibularis trigemini.
m. i. Ramus mandibularis internus facialis.
o.—Nervus opticus. *o. m.*—Nervus oculomotorius.
o. p.—Ramus ophthalmicus profundus trigemini.
o. q.—Os quadratum.
o. s.—R. ophthalmicus superficialis facialis. *p.*—Os parietale.
pp.—Os palatopterygoideum. *ps.*—Os parasphenoideum.
q.—Quadratum. *r. c.*—Ramus communicans glossopharyngei.
s.—Os squamosum. *t.*—Trabeculum.

the squamosum, who does not however, give the relation of the nervus facialis. DRÜNER has recently described correctly the relations in both Necturus and Proteus.

[1] COPE, E. D. The Batrachia of North America. *Bull. U. S. Nat'l. Museum*, No. 34, 18

The following description of the relations in a Necturus of 49.5 mm. length, based in part on a model of this stage (Fig. 1), will serve as a basis of comparison. The operculum at this stage is roughly oval in outline and slighly ridged along its long axis. At its cephalic end it is fused with the otic capsule, projecting backward into the fenestra vestibuli. From the cephalic end a dense ligament passes cephalad and dorsad to the os squamosum at about its middle point. The bone forms a slight curve, the convexity looking upwards, and it lies upon the external semicircular canal of the otic capsule, extending down over the otic process of the quadrate and becoming closely connected with a bone lying upon the external surface of the quadratum, and which it partly covers. This bone[1] I shall describe in another place. The squamoso-opercular ligament is attached to the under side of the squamosum where the bone passes from the ear capsule to cover the outer side of the processus oticus quadrati. At this stage the "stapedial" process of the squamosum present in the adult has just begun to develop. The ligament, in its course from the operculum to the squamosum, passes external (laterad) to the ramus jugularis facialis and the vena jugularis. The ramus jugularis passes outward and slightly backward, between the ligament and the vein to the dorsal edge of the former where it receives the ramus communicans glossopharyngei, which lies close to the ear capsule laterad to the vena jugularis. Beyond the point of the union with the ramus communicans, the jugular branch of the seventh passes outward, under the ventral edge of the squamosum to curve around the dorsal side of the otic division of the M. depressor mandibuli. The ramus mandibularis externus facialis from its ganglion which lies immediately outside the foramen for the facial nerve, in a depression just caudad of the

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[1] This bone arises in Necturus as a separate ossification, whose lower end subsequently is fused with or becomes the ossification of the quadrate. In Desmognathus and Spelerpes the same bone lies farther back, projecting under the squamosum, and in the adult forms the process of the quadrate named for he purposes of this paper the subsquamosal process.

processus basilaris quadrati, passes forward and outward under the quadratum to the outer surface of the squamosum, passing in front of (ventrad and cephalad to) the ligament.

The ramus palatinus which passes forward through a foramen distinct from that for the rest of the facial nerve, and the ramus mandibularis internus which passes immediately ventrad from the cephalic edge of the accessory lateral line ganglion, do not come into close relation to the columella, but are, of course, morphologically below and in front of it.

In an older Necturus, 9.4 c.m. long, the relations are as in the specimen just described, save that the processus "stapedialis" of the squamosum has attained an appreciable length, and the operculum possesses a short ossified stalk to which the liga-

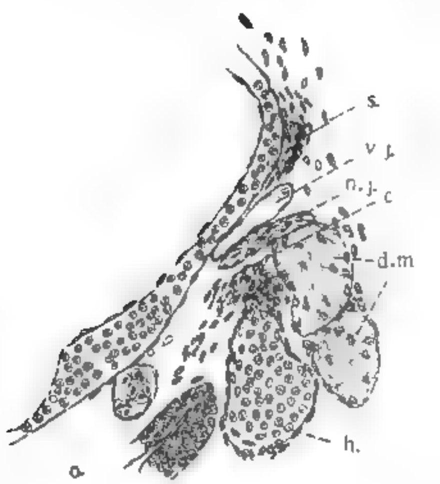

Fig. 2a. Section of the Necturus embryo 19 mm. in length. *c.*—anlage of the squamoso-columellar ligament; *h.*—hyoid; *v. j.*—vena jugularis ; *n. j.*—nervus jugularis ; *d. m.*—M. depressor mandibuli ; *s.*—squamosum.

Fig. 2b. Same, three sections farther forward.

ment attaches. Neither ossification appears to be an ossification of the ligament, but ossifications of the squamosum and operculum at each end of the ligament, acomplishing in that way the increase in length due to growth. In the adult, the operculum possesses an ossified process of some length joined

[redacted]

by ligament to the relatively long stapedial process of the squamosum.

That the relation of ligament to squamosum is a primary condition in this form and not a secondary modification, is seen in tracing the development of these structures. In an embryo 19 mm. in length (Fig. 2), the ossification of the squamosum is just beginning as a formation in a group of cells located upon the external semicircular canal of the ear. It extends down over the otic process of the quadratum covering with its lower (cephalic) end the upper end of a bone which is developed upon the external surface of the quadrate. At this stage, the operculum is just beginning to chondrify as a distinct center, and from it a cord of cells is continued forward, ventral to the vena jugularis and the ramus jugularis, to the cell surrounding the developing squamosum, becoming continuous with them a short distance (50μ) back of the processus oticus quadrati. The cells are of course continuous with those of the squamosum and also with the cells between that bone and the quadratum, so that the squamosum, the quadratum, and the ligament-anlage, may be said to be joined together by a common mass of cells. In the just hatched larva, likewise, the ligament-anlage, clearly goes to the under side of the squamosum and inserts itself between that bone and the processus oticus quadrati, so that it might be interpreted as going to both structures. As soon as the connective tissue fibers develop, however, the relation is seen to be with the squamosum and not with the quadratum. It is interesting to note the relatively early development of the ligament —practically at the same time as the squamosum and the operculum—later, however, than the chondrification of the chondrocranium.

Spelerpes bilineatus. In this form, as well as in Desmognathus, the suspensorio-opercular connection possesses the same relation to the nervus facialis—that is, the nerve lies entirely cephalad and ventrad to the stilus columellae; in other words, under it. In relation to the jugular vein, the stilus possesses the same relation as the ligament described in Necturus—i. e. it passes ventrad to it.

In the adult Spelerpes (Figure 3), the stilus is cartilaginous with a perichondral ossification continuous with the ossification of the operculum;—the cartilaginous core of the stilus, however, is distinct from the ring of cartilage within the operculum.

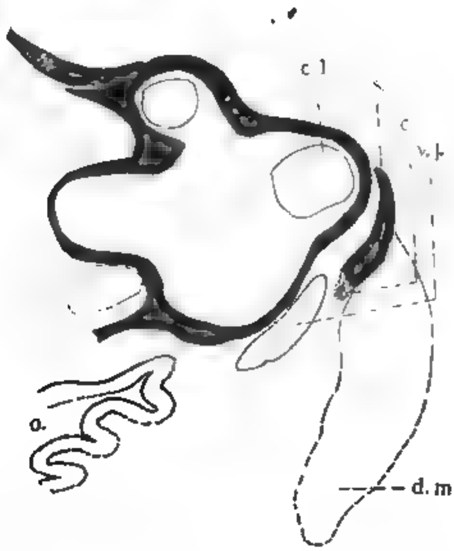

Fig. 3. Spelerpes bilineatus, adult 67 mm. long. Section through the right otic capsule. *c*—Stilus columellae; *o*—oral cavity; *v. j.*—vena jugularis; *d. m.*—M. depressor mandibuli; *S.*—squamosum.

The stilus passes forward, upward and slightly outward to the lower edge of the squamosum with which its cephalic end is joined by connective tissue (Fig. 3), and also with a small cartilage which lies upon the ventral edge of the squamosum. This cartilage extends forward for about 150 microns and is cylindrical. It is free at its caudal end, which articulates with the stilus, and fused with the ventral edge of the squamosum. The stilus and operculum are at about the same level. The former lies at first upon the dorsal side of the external semicircular canal, gradually moving down to the lateral surface of the otic capsule, as it is traced forward. As it continues to

shift its position ventrally to pass to the outer surface of the quadratum, it becomes farther separated from the ear capsule leaving a space in which the quadratum appears. The ventral (lateral) edge of the squamosum is thin where the bone rests upon the ear capsule, but becomes thicker as the bone leaves that structure, i. e. where the stilus articulates with it, becoming thinner again as the bone applies itself to the quadratum.

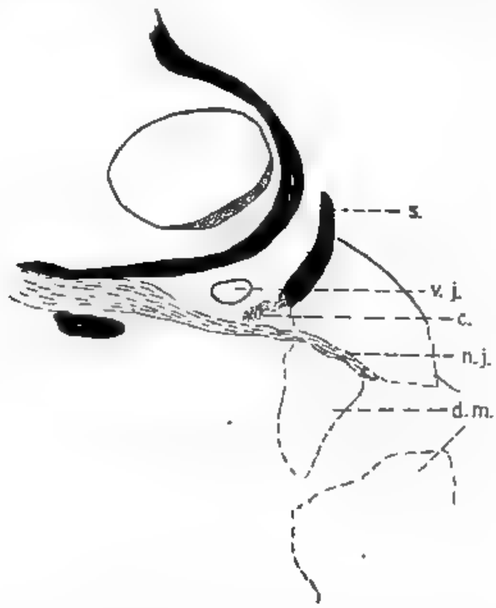

Fig. 4. Larval Spelerpes bilineatus, 43 mm. long; *c.*—stilus columellae; *v. j.*—vena jugularis; *n. j.*—nervus jugularis; *d. m.*—M. depressor mandibuli; *s.* Squamosum.

In the interval between the squamosum and the ear capsule, two processes of the quadratum extend backward, (1) a bony process applied immediately to the inner surface of the squamosum, extending back to the level of the cephalic end of the cartilage upon the ventral edge of the squamosum, and (2) a short cartilaginous process lying between the bony process and the ear capsule. The latter seems to be a part of the (morphologically) basilar process of the quadratum and is very short.

Neither one comes into relation to the columella as do the corresponding processes in Desmognathus.

Larval Spelerpes of 25 mm., 35 mm., 43 mm. (Fig. 4) and 60 mm. in length, were examined in this connection and showed that the relation between columella and squamosum in this form (Fig. 4) is a primary one, as in Necturus. In the 25 mm. larva, the suspensorio-opercular connection is represented by a cord of cells which passes from the operculum forward and upward to the ventral edge of the squamosum. This cell cord lies ventrad to the vena jugularis around which it curves, closely applied to the vein, compressed between it and the R. jugularis facialis, the relation of nerve and suspensorio-opercular connection being thus the opposite of that in Necturus. Compare Figs. 2 and 4. In a 35 mm. larva cartilage has appeared in the cord of cells, otherwise the relations are essentially the same as in the younger larva, while in the 43 mm. specimen ossification of the stilus has begun, continuous with the perichondral ossification of the operculum.

The facial nerve, as has been said, lies entirely cephalad and ventrad to the suspensorio-opercular connection. The only branch which comes into contact with the stilus is the ramus jugularis which in the larva passes close to the ventral border of that structure. The ramus communicans glossopharyngei likewise, passes below the stilus, curving around it from its dorsal side in a course forward to join the facial. In the adult neither nerve is in as close relation to the stilus as in the larva.

The origin and significance of the small cartilage applied to the ventral border of the squamosum is obscure because of the absence of transforming and young adult material. In the larva it is not present.

With the exception of the R. jugularis and R. communicans, then, the suspensorio-opercular connection in Spelerpes has the same morphological relations as the ligament in Necturus.

Desmognathus fusca. (76 mm.) In this form it would seem as if, as compared with Spelerpes, the suspensorium were

displaced backward in relation to the operculum, so that the stilus is shorter, passes more directly outward and upward, and is joined more closely with the subsquamosal process of the quadrate (Fig. 5) than with the squamosum itself. It is,

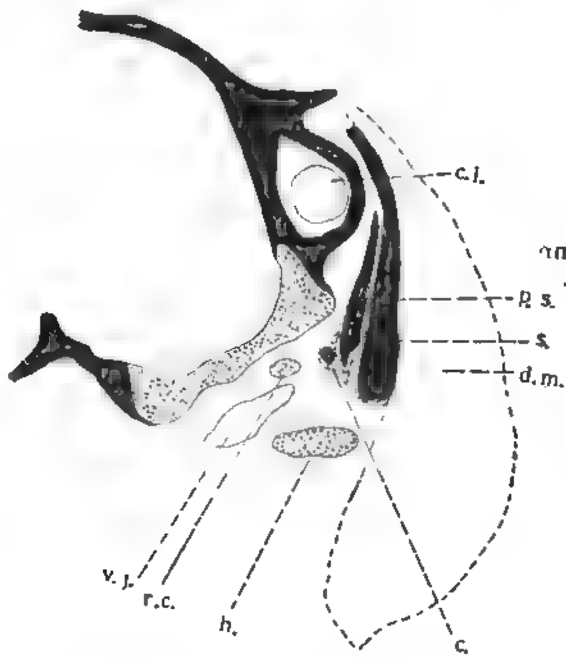

Fig. 5. Desmognathus fusca, adult, 76 mm. *c*—stilus columellae; *c. l.*—canalis lateralis; *h.*—hyoid; *v.* j.—vena jugularis; *r. c.*—ramus communicans; *d. m.*—depressor mandibuli; *p. s.*—subsquamosal process of quadratum; *s.*— squamosum.

however, joined to both bones by connective tissue, and with the cartilaginous process of the quadrate. This process is longer than the corresponding process in Spelerpes and is separated from the stilus by an interval of but (ca.) 50 μ (Fig. 6) The squamosum and the subsquamosal process of the quadrate are essentially the same as in Spelerpes. Stilus and operculum are as in Spelerpes, though the cartilage in the columella is small.

Turning to the larval form for an interpretation of the condition in the adult, we find in a specimen 21 mm. in length, that the suspensorio-opercular connection is at this stage cellular and extends from the cephalic border of the operculum to the squamosum as a dense cord of cells. It has the same rela-

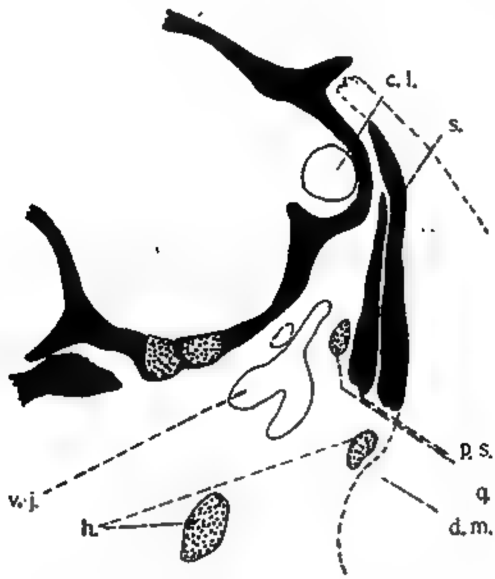

Fig. 6. Same, three sections (75 μ) farther forward; *q.*—cartilaginous (columellar) process of the quadrate.

tion to the jugular nerve and vein as in Spelerpes, though it does not come into as close contact with either as in that form. Its cephalic end is rather difficult to determine (Fig. 7), since the anlage is continued forward to join the subsquamosal process (of the quadrate) which at this stage is a distinct bone, so that it may be said to be connected with both bones. There is, however, no direct connection with the (cartilaginous) quadrate, and from the conditions in Necturus and Spelerpes, we are warranted, I think, in emphasizing the connection with the squamosum rather than that with the subsquamosal process of the quadrate which, in fact, is not as direct. In a larva 33

mm. in length (Fig. 7), apparently approaching the period of transformation, the relations are as in the younger specimen save that cartilage has appeared in the suspensorio-opercular connection as a center distinct from the cartilage of the operc-

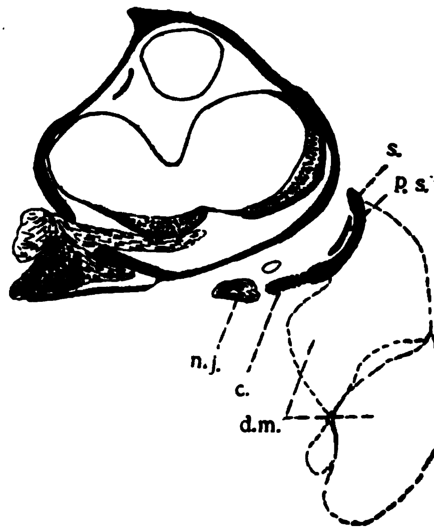

Fig. 7a. Larval Desmognathus fusca, 33 mm.; *c.*—stilus columellae; *v. j.*—vena jugularis; *n. j.*—nervus jugularis (R. communicans); *d. m.*—M. depressor mandibuli; *p. s.*—subsquamosal process of the quadrate; *s.*—squamosum.

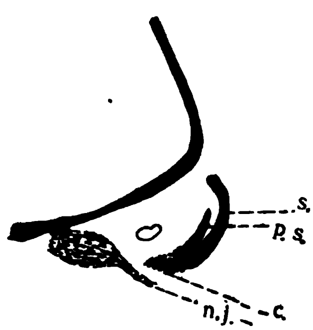

Fig. 7b. Same; three sections farther forward.

ulum. In a small adult (27 mm.), presumably but recently transformed, the cartilaginous stilus is connected more directly with the squamosum, but also by dense connective tissue with

the subsquamosal and the short cartilaginous processes of the quadrate. The shifting of the attachment takes place in the growth of the adult rather than at the transformation of the larva.

Amphiuma means (51 mm). Through the courtesy of my co-worker, Professor H. W. NORRIS, I am enabled to give here the following brief statement of the relations occurring in Amphiuma as found by him and verified by myself in his preparations. This form is interesting because it possesses a continuous cartilaginous connection between the quadrate and operculum, as described by WIEDERSHEIM,[1] HAY,[2] and WINSLOW.[3] This has been spoken of as the columella, and as the stapedial process of the quadrate. It evidently, however, represents both the columella (stilus columellae) and the primarily cartilaginous process of the quadrate found in Desmognathus. The articulation in the specimen upon which this statement of relations is based is much closer than it is in Desmognathus, and in older specimens undoubtedly, as described, there occurs a fusion of the two structures to form one continuous rod between the operculum and the quadratum. In this specimen, the stilus is a cartilaginous process of the operculum which is itself cartilaginous. The stilus columellae goes forward and slightly upward to become applied to the thickened ventral border of the squamosum to which it is joined by connective tissue. It is succeeded by the cartilaginous columellar process of the quadrate to which it is very closely connected. This process lies also against the ventral edge of the squamosum and slightly on its inner side. The connection of the stilus, therefore, is with the squamosum and the cartilaginous process of the quadrate and not at all with the ossification which (from the condition in the adult Desmognathus and Spelerpes) I have spoken of as the subsquamosal process of the os quadratum.

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[1] Op. cit., p. 502.

[2] '90, HAY, O. P. The Skeletal Anatomy of Amphiuma during its earlier Stages. *Journ. Morph.*, Vol. IV.

[3] '98, WINSLOW, G. M. The Chondrocranium in the Ichthyopsida. *Tufts College Studies*, No. 5, 1898.

All branches of the facial nerve pass below the stilus columellae (and stapedial process of the quadrate) as has already been stated by HAY, instead of over it.[1]

Other Urodela. In Menopoma (Cryptobranchus) alone is the relation of columella to the squamosum described by WIEDERSHEIM,[2] and also by PARKER.[3]

In *Amblystoma* I can only state that there is present in the larva a cord of cells, passing from the operculum to the ventral border of the squamosum, which from the position and relation (dorsal) to the facial nerve is undoubtedly the anlage of the suspensorio-opercular connection. This relation of the "columella" to the facial nerve, has already been affirmed by HASSE and PARKER.

Proteus anguineus. Opportunity for studying the relations in this form was afforded me by the generosity of Professor WIEDERSHEIM. As might be expected from the published figures (WIEDERSHEIM; op. cit., Fig. 19), the relations in Necturus and Proteus are the same. There is a strong squamoso-opercular ligament passing from the stapedial process of the squamosum to the short stilus columellae, and to this the branches of the facial nerve have the same relation as in Necturus; R. jugularis passes above the ligament, R. mandibularis externus below it.

Nervus facialis.[4]

Since the homology of the chorda tympani is closely connected with that of the relations and connections of the columella auris, the following brief account of the course of the branches of the facial nerve is offered. The relations of the nerve in the larvae only of Desmognathus and Spelerpes have

[1] This is also in accord with KINGSLEY'S description. (*Tuft's College Studies, No. 7, p. 305.*)

[2] Op. Cit., p. 502.

[3] Op. Cit., Pt. III, p. 184.

[4] The following names of the branches of the facial nerve are used: R. palatinus; R. jugularis (FISCHER); R. mandibularis internus (R. Alveolaris, FISCHER); R. mandibularis externus (R. mentalis, FISCHER).

been studied, as the changes at transformation introduce complexities unimportant in this connection.

Necturus (9.4 cm.). The ganglion geniculi is intra-cranial, in the beginning of what might be described as a short facial canal, adjoining and cephalad of the cephalic division of the auditory nerve. From this ganglion the ramus palatinus arises as a small nerve which passes cephalad and ventrad through a separate foramen, and goes cephalad at the side of the trabecula, finally passing ventrad between the parasphenoid and the pterygo-palatinum to the roof of the oral cavity. The remainder of the nerve passes laterad through its foramen and develops a second ganglion, which undoubtedly belongs to the R. mandibularis externus, a part of the lateral line component. At this ganglion the nerve divides into two branches, R. mandibularis facialis, and R. jugularis; the former divides, as soon as it leaves the ganglion into the Rami mandibularis externus and internus. The R. jugularis passes upon the caudal side of the ganglion and has but little if any connection with it. Its course is nearly directly laterad for a short distance, passing dorsad to the ligament between that structure and the jugular vein; beyond the ligament, under the ventral edge of the squamosum it turns ventrad and caudad around the dorsal border of the otic division of the M. depressor mandibuli to pass under the fascia covering the lateral surface of that muscle. At the lateral border of the M. mylohyoideus posterior, it passes to the ventral side of that muscle. It innervates the M. depressor mandibuli, ceratohyoideus, and mylohyoideus posterior. The Ramus communicans glossopharyngei passes forward from the ganglion complex of the IX and X and joins the R. jugularis just beyond the point where it emerges above the columella. The M. depressor mandibuli gains some at least of its innervation from fibers of the R. jugularis which pass back along the R. communicans. R. jugularis seems to be purely a motor nerve, though it is possible that it may have a small lateral line component.

The R. mandibularis externus goes cephalad, laterad and ventrad under the ventral border of the squamosum below (in front of) the point of attachment of the ligament curving

around to the outer surface of the squamosum. After giving a branch to the skin whose destination was undoubtedly the lateral line sense organs, it divides into two branches, one[1] passing farther caudad and mesad, so as to lie on the mesal side of the lower jaw, between the M. submaxillaris and the skin; the other passing to the outer side of the lower jaw. From these two branches, evidently the lines of sense organs called by me[2] gular, and oral (incl. angular) respectively, receive their innervation. It is possible that the gular division contains communis fibers as well as those destined for the lateral line organs. The M. submaxillaris I find to be innervated by the trigeminus (R. mandibularis internus V), in this supporting Miss PLATT[3] as against RUGE.[4] Both divisions are subcutaneous,—i. e. external to all skeletal and muscular structure.

The ramus mandibularis internus, separates from the R. mandibularis externus as it leaves its ganglion, and passes ventrad and cephalad, on the inner (ventral) side of the quadrate soon passing through the suspensorio hyoid ligament. This is the condition in a specimen 9.4 centimeters in length. In younger specimens the nerve seems to lie on the outer side of the ligament, though very closely applied to it. Beyond the

[1] This is evidently the branch described by VON PLESSEN and RABINOVICZ (Die Kopfnerven von Salamandra maculosa im vorgerückten Embryostadium, 1891) as "Begleiter des R. hyoideo-mandibularis (h. m')"—Hyomandibularis accessorius. By some these branches have been incorrectly called Rami mandibularis internus (alveolaris) and externus. The homology of either of these nerves with the chorda tympani, suggested by HERRICK in his '94 paper (Amblystoma punctatum) and accepted by KINGSLEY '02, for Amphiuma, can, of course, hardly hold now. COGHILL calls these, Rami mentales externus and internus.

[2] '95. KINGSBURY, B. F. The Lateral Line System of Sense-organs in some American Salamanders, and Comparison with the Dipnoans. *Proc. Americ. Micr. Soc.*, Vol. XVII, 1895.

[3] '98. PLATT, JULIA B. The Development of the Cartilaginous Skull and of the Branchial and Hypoglossal-Musculature in Necturus. *Morph. Jahrb.*, Bd. XXV, 1898.

[4] '96. RUGE, G. Ueber das peripherische Gebiet des Nervus facialis bei Wirbelthieren. *Festschrift für Carl Gegenbaur*, 1896, pp. 195-348.

ligament, the nerve is on the inner side of the M. depressor mandibuli, MECKEL's cartilage and the os articulare successively. It is separated by connective tissue from the mucous membrane of the mouth which it gradually approaches, lying on the dorsal (mandibular) side of the depression[1] between the hyoid and mandibular arches. At about the level of the caudal border of the eye, it divides into two branches, one of which continues forward on the inner side of the jaw, the other moves farther ventrad and mesad; both, however, become compressed between the M. submaxillaris and the oral mucous membrane of the floor on the mouth between the hyoid (tongue) and the mandible.

No communication occurs between this nerve and the Ramus mandibularis internus of the fifth.

In the larvae of Spelerpes[2] and Desmognathus the relations of the four main branches of the seventh nerve are in general essentially as in Necturus. The Ramus jugularis, however, instead of curving around the dorsal border of the otic division of the depressor mandibuli as in Necturus, in Spelerpes passes through that division of the muscle, while in Desmognathus, it passes *under* the *entire* muscle. In both Desmognathus and Spelerpes it contains a cutaneous—undoubtedly lateral line—component which was not found in Necturus. As in Necturus the M. depressor mandibuli receives its innervation from fibers that accompany the Ramus communicans. The relation of both the R. jugularis and the R. communicans to the stilus columellae has been spoken of in connection with that structure.

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[1] "The *R. alveolaris VII*, composed wholly of communis fibers, follows the posterior border of the suspensorium to the angle of the jaw. Along this part of its course, the R. alveolaris lies mesially of the hyo-suspensorial ligament, and anteriorly of the deep pharyngeal evagination which represents the embryonic spiracular cleft." '02, COGHILL, G. E. The Cranial Nerves of Amblystoma tigrinum. *Journ. Comp. Neurol.*, Vol. XII, p. 228.

[2] The branches and distribution of the facialis in the larval Spelerpes have been correctly given by Miss M. A. BOWERS: The Peripheral Distribution of the Cranial Nerves of Spelerpes bilineatus. *Proc. Am. Acad. Arts and Sci.*, Vol. XXXVI, 1900.

The Ramus mandibularis externus passes cephalad and laterad around the lower edge of the squamosum to its outer surface, where it divides into branches, as in Necturus, one of which curves ventrally over the outer surface of the M. depressor mandibuli and its tendon to run forward upon the ventral surface of the M. submaxillaris. The other division runs cephalad upon the outer side of the lower jaw. Both seem to be purely lateral line nerves.

The R. mandibularis internus separates from the externus at the cephalic border of the ganglion and goes laterad cephalad and ventrad immediately to the mucous membrane of the oral cavity between the hyoid arch and the quadrate and (farther cephalad) the mandible. In the first part of its course it lies in the connective tissue between the oral mucous membrane, the quadrate and the M. depressor mandibuli, the quadrate lying dorsally and the muscle laterally. Farther cephalad it passes on the inner side of the suspensorio-hyoid ligament, MECKEL's cartilage and the os articulare on whose mesal side it divides, one branch passing through a canal in that bone to join the R. circumflexus V,[1] which at nearly the same level passes between the os dentare and MECKEL's cartilage. This soon divides on emerging from its canal into the R. submaxillaris and R. mandibularis internus V. The remainder of the R. mandibularis internus VII runs forward between the mucous membrane and the mandible. At the level of the appearance of the M. submaxillaris, it is compressed between that muscle and the mucous membrane of the floor of the mouth. The portion of the R. mandibularis internus VII which joined the trigeminus I was unable to trace. I was unable to trace the fibers of the R. mandibularis internus in any of the forms even into the neighborhood of taste buds. It is clear, that the R. mandibularis internus (alveolaris) in Urodeles has practically the same course, the only marked differences being that in Necturus, and Proteus, it does not pass through a canal in the

[1] I use the name applied to the comparable nerve in the frog, believing them homologous. Compare, however, COGHILL, op. cit., pp. 265 and 266.

os articulare (angulare?), while in Amphiuma,[1] ('02, KINGSLEY), Desmognathus and Spelerpes, Amblystoma, Salamandra and Triton, (COGHILL, op. cit., p. 269), it occupies such a canal. In Necturus, Proteus, and Amphiuma (KINGSLEY) it does not anastomose with the Vth, while in the other forms it does.

From the above relations it is seen that the only nerve which can be considered as a homologue of the chorda tympani is the Ramus mandibularis internus VII which goes to the mucous membrane of the floor of the mouth between the hyoid and mandibular arches.[2] This, of course, is the homology already advanced by GAUPP,[3] STRONG[4] and others, GAUPP from morphological relations, STRONG from the character of the fibers and their destination. ALLIS,[5] HERRICK[6] and GREEN[7] have since seen reason to doubt the homology on the grounds of the pretrematic position which the homologue of the chorda tympani must have, the nerve identified by them as R. mandibularis internus facialis being a post-spiracular nerve, and a Ramus facialis pretrematicus being chosen by them as the homologue of the chorda tympani.

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[1] '02, KINGSLEY, J. S. The Cranial Nerves of Amphiuma. *Tufts College Studies*, No. 7, pp. 293-321.

[2] RUGE (op. cit., p. 294) recognizes this nerve as the chorda tympani though he does not identify it as the internal mandibular (alveolaris, FISHER) but seems to find that also present as a cutaneous nerve. COGHILL (op. cit.) regards it as a homologue of the chorda tympani.

[3] '93, GAUPP, E. Beiträge zur Morphologie des Schädels. I. Primordial Cranium und Kieferbogen von Rana fusca. *Morph. Arbeiten* herausg. VON G. SCHWALBE, Bd. II.

[4] '95, STRONG, O. S. The Cranial Nerves of Amphibia. A Contribution to the Morphology of the Vertebrate Nervous System. *Journ. of Morph.*, Vol. X.

[5] '97, ALLIS, E. P. The Cranial Muscles and Cranial and first Spinal Nerves in Amia calva. *Journ. of Morph.*, Vol. XII, No. 3, 1897.

[6] '99, HERRICK, C. J. The Cranial and First Spinal Nerves of Menidia; a Contribution upon the Nerve Components of the Bony Fishes. *Journ. Comp. Neurol.*, Vol. IX, 3-4.

[7] '00, GREEN, H. A. On the Homologies of the Chorda Tympani in Selachians. *Journ. Comp. Neurol.*, Vol. X, 4.

The question seems to me to involve the correctness of the interpretation of the chorda tympani as pretrematic, and the homology of the mandibularis internus VII, in Menidia, Amia and Selachia, which appears to have a course somewhat different from that of the branch in Urodeles. For a comparison of the relations in fishes and Amphibia, the effect of the morphological differences in the suspension of the jaw and the value of the relation of nerves to skeletal structures in determining their homology, are involved; and for the larger question of the chorda tympani, the homology of the sound-transmitting apparatus in the different classes, as well; so that it seems to me a close consideration of homologies is yet premature.

The pre- or post trematic origin of the R. mandibularis internus in Urodeles cannot, of course, be determined, since the first gill cleft does not come to development. From its point of origin and course, it certainly could be pretrematic, as COLE[1] has pointed out, and it seems to me the possibility that this nerve represents a pre-trematic nerve such as GREEN, (e. g.) described in Selachia,[2] is worth considering. In this connection the different relations of the facial nerve and columella auris in Anura and Urodela must also be considered. There is here presented in allied forms, a difference of relation

[1] '96, COLE, F. J. On the Cranial Nerves of Chimaera monstrosa (Linn) with a Discussion of the Lateral Line System and of the Morphology of the Chorda Tympani. *Trans. Roy Soc.*, Edinburgh, Vol. XXXVIII, Pt. III, (No. 19).

[2] I have already referred to the statement by COGHILL (p. 228) that this nerve could be considered pre-trematic. In the forms studied by me, however, the conditions, I believe, hardly warrant a definite conclusion. COGHILL, even, would regard the R. mandibularis internus in Urodela and Anura, as not homologous (p. 265), and this, too, seems to me rather extreme. The entire hyomandibular nerve in the frog crosses over and behind the columella auris and in Urodela under and in front of it. As stated in a previous paper ('95, The Structure and Morphology of the Oblongata in Fishes; *Journ. Comp. Neurol.*, Vol. VII, p. 30) where I quote also the opinion of Miss PLATT to that effect, I feel that the origin and distribution of a nerve are of more importance than its course, which may vary, and consequently should not be too closely made the basis of homologies. We also see that the relation of a nerve to a muscle cannot be relied upon as a test.

of nerve to skeletal structure of extreme type. As is well known,[1] in the frog the hyomandibular nerve crosses above the columella and passes down behind it to its destination, whereas in Urodeles it passes in front of or below the same structure. Other cases of similar differences of relation in this region, mentioned in this paper, are (a), the relation of the jugular nerve in Necturus on the one hand and in the other salamanders investigated on the other hand; in the first case it passes above the columella (stilus columellae), in the second, below. (b), Necturus also offers a difference in the relation of the internal mandibular branch to the quadrato-hyoid ligament. In Desmognathus and Spelerpes the nerve passes on the inner side of the ligament; in Necturus, through the ligament, or on its outer side in younger individuals. Further (c), the R. jugularis in Necturus passes over the depressor mandibuli; in Spelerpes larvae, through it; in Desmognathus larvae, under it.

The differences, in the last two cases at least, it seems to me, might possibly be explained on a more or less mechanical basis. The nerves (and muscles) are already developed and their course and positions established before the anlage of the columella or that of the quadrato-hyoid ligament has appeared, and the relations the latter structures assume when they do develop, has been determined for them by the position of the structures earlier developed. This explanation would not, of course, be an ultimate one.

The nomenclature employed in the above descriptions is that suggested by Professor GAUPP. *Columella*, including operculum and its process, *stilus columellae*, which may be joined to the suspensorium by an appreciable ligament—*ligamentum suspensorio-columellare* (*operculare*). I regard the suspensorio-columellar (opercular) connection in the forms studied as homologous. The term stilus columellae is used in describ-

[1] '93, GAUPP, E. Beiträge zur Morphologie des Schadels. I. Primordial Cranium und Kieferbogen von Rana fusca. *Morph. Arbeiten*, herausgegeben von G. Schwalbe, Bd. II.

'99. ECKER'S u. R. WIEDERSHEIM'S Anatomie des Frosches, auf Grund eigener Untersuchungen durchaus neu bearbeitet. II Abth. 1899.

ing the relations in Desmognathus and Spelerpes, in view of the structure in the adult, despite the fact that the "stilus" probably begins as a chondrification in the cord of cells extending from the operculum to the squamosum. This point of a separate chondrification, however, has not been firmly established. In that case the ligamentum squamoso-columellare (operculare) and the stilus columellae of Spelerpes I should regard as homologous—despite the different relations to the facial nerve.

In conclusion, I may say that the points which I wish to emphasize are:

(1) The primary connection of the columella with the bone which I regard as the squamosum.

(2) The different relations of the facial nerve to the ("squamoso-opercular" connection) stilus columellaris in the frog, Necturus (and Proteus) and other Urodela.

(3) The secondary nature of the connection of the columella with the quadrate cartilage, where such connection occurs.

(4) The different relations of the ramus jugularis VII, to the musculus depressor mandibuli in Necturus, Spelerpes, and Desmognathus.

(5) The course and relations of the R. mandibularis internus VII, in view of the possible homology with the chorda tympani.

(6) The question of the value of the relation of a nerve to skeletal parts and muscles, as a criterion of homology.

Anatomisches Institute, Freiburg i. B., May 1, 1902.
Cornell University, Sept., 1903.

The Columella Auris in Amphibia

by B. F. KINGSBURY and H. D. REED
From the Histological Laboratory, Cornell University,
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With Seven Figures.

The following is a preliminary communication of the results obtained by us in a study of the relations and connections of the sound-transmitting apparatus in certain American Urodeles.

Since it is in the class Amphibia that a sound-transmitting apparatus first appears, a knowledge of the relations here is of double value,—in aiding the interpretation of homologies in the lower forms (fishes), and in contributing toward the solution of the difficult questions surrounding the significance of the reptilian columella and the auditory ossicles of the Mammalia. Furthermore, the function of the Amphibian columella is unknown, and as a preliminary to experimental work its relations in a large series of forms were ascertained.

Gaupp[1] has already called attention to the apparently different relation that the columella has to other structures in Urodeles, which led him to believe that there were two different connections of this element found in these forms, and later[2] he restated this opinion. Drüner[3] has

[1]Gaupp, E. Onotogenese und Phylogenese des Schallleitenden Apparates bei den Wirbeltieren. Merkel u. Bonnet: Ergebnisse der Anat. u. Entw., Bd. VIII, 1898-1899.

[2]Gaupp, E. Die Entwicklung des Kopfskelettes. Hertwig's Handbuch der Entwickelungslehre der Wirbeltiere, Bd. III, p. 696.

[3]Drüner, L. Studien zur Anatomie der Zungenbein-, Kiemenbogen- und Kehlkopf-Muskeln der Urodelen. I. Teil, Zool. Jahrb., Abt. f. Anat. u. Ont. d. Tiere, Bd. XV, H. 3, 1901.

likewise expressed this interpretation. This opinion was based especially upon the statements of Huxley,[4] Wiedersheim,[5] Parker[6] and Hasse.[7] Thus Huxley described in Necturus a "suspensorial stapedial ligament" under the facial nerve. Wiedersheim gives as the universal condition that a connection between the operculum and quadrate existed below the facial nerve. Hasse, on the other hand, in Siredon described the nerve as under the columella, while Parker in the large number of forms studied by him apparently found both connections, although it is sometimes difficult to determine what relation he wished to imply.

In 1903 one of us[8] described in detail the early development of the columella in Necturus and there called attention to the fact that almost from its first appearance it was connected with the squamosum (Paraquadratum of Gaupp) by a cord of cells where later was established a strong ligamentous connection. Believing that the early and primary connection of the columella with the squamosum was of fundamental morphologic importance, we have undertaken to ascertain the connections and development of the columella in a large number of representative Urodeles.

The forms studied are: Necturus maculosus, Proteus anguineus, Amphiuma means, Ambystoma (Amblystoma) punctatum, Hemidactylum scutatum, Plethodon cinereus erythronotus, Gyrinophilus porphyriticus, Spelerpes bilineatus, Diemictylus viridescens. To these we propose to add: Siren, Cryptobranchus, Chondrotus, Autodax, Manculus, Salamandra, Triton. It is recognized that the relations of the columella to other structures in many of these forms have been described by earlier workers, but it was thought that re-examination by serial sections and models would give us a better basis for interpretation.

[4]Huxley, T. H. On the Structure of the skull and of the Heart of Menobranchus lateralis. Proc. Zool. Soc., 1874.

[5]Wiedersheim, R. Das Kopfskelett der Urodelen. Morphol. Jahrb., 1877.

[6]Parker, W. K. On the Structure and Development of the Skull in the Urodelous Amphibia, Part I, Trans. Philo. Soc., Vol. CLXVII, Part 2, 1877. On the Morphology of the Skull in the Amphibia Urodela, Trans. Linn. Soc., Series 2, Vol. II, Pt. 3, 1882. On the Structure and Development of the Skull in Urodeles, Trans. Zool. Soc., Vol. XI, Pt. 6, 1882.

[7]Hasse, C. Ueber den Bau des Gehörorgans von Siredon pisciformis und über der vergleichenden Anatomie des Kiefersuspensoriums, Anatom. Studien, herausg. von C. Hasse, Vol. I, 1872.

[8]Kingsbury, B. F. Columella Auris and Nervus Facialis in the Urodela. Jour. Comp. Neurol., Vol. XIII, pp. 313-334.

As a result of this work, we have found that in Necturus, Ambystoma, Hemidactylum, Plethodon, Gyrinophilus, Spelerpes and Desmognathus the columella is connected with the squamosum. This connection arises very early in Necturus, Amphiuma, Ambystoma, Plethodon, Spelerpes and Desmognathus. Early stages of the others have not been examined. A very large number of stages of Ambystoma punctatum[9] from the early embryo through the larval, transforming and adult periods have been examined. A brief statement of the development and relations of the columella auris in this form will be given, since we have made it the basis of comparison.

The columella first appears in embryos from 4-6 mm. long at a time soon after the chondrification of the ear capsule. It is developed as a separate nodule of cartilage resting on the membrane of the fenestra vestibuli and connected with the squamosum by a dense tissue rich in cells, under and close to the jugular vein. It apparently develops outside the ear capsule. This result, which is different from that gained by Stöhr in 1888 in Siredon, is nevertheless in agreement with the development of the columella in Necturus as described by Platt.[10]

During the larval period the cephalic end of the columella becomes fused with the fenestra vestibuli. The connection with the squamosal persists and becomes a very strongly developed tissue which appears to be fibro-cartilage (Figs. 1 and 2, lc.). The relation of the ligamentum squamoso-columellare to the carotid artery and jugular vein is that found in all forms; *i. e.,* above the former and below the latter (Fig. 3, lc. and vj.). In all forms examined the facial nerve passes below the ligament except in Necturus and Proteus, where one branch, r. jugularis, passes above it.

We wish to emphasize the fact that in Ambystoma we encounter the same early established relations of the ligamentum squamoso-columellare as in Necturus, and in spite of the somewhat different relations of the facial nerve in the latter we believe that the connections are homologous.

[9]Through the courtesy of Professor S. H. Gage, who placed at our disposal the excellent series of larval Ambystoma in the collection of the Department of Histology, we were enabled to make complete our series of stages in this form, for which we wish to express our appreciation.

[10]Platt, Julia B. The development of the cartilaginous skull and of the branchial and hyoglossal musculature in Necturus. Morph. Jahrb., Bd. XXV, Heft 3, 1897.

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The columella first appears in embryos from 4-6 mm. long at a time soon after the chondrification of the ear capsule. It is developed as a separate nodule of cartilage resting on the membrane of the fenestra vestibuli and connected with the squamosum by a dense tissue rich in cells, under and close to the jugular vein. It apparently develops outside the ear capsule. This result, which is different from that gained by Stöhr in 1888 in Siredon, is nevertheless in agreement with the development of the columella in Necturus as described by Platt.[10]

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At transformation very remarkable changes occur, which appeal to us as profoundly significant in interpreting the homologies of the sound-transmitting apparatus. These changes are:

(*a*) An extension of the fenestra vestibuli backwards.

(*b*) Largely, at least, from the walls of the ear capsule a new operculum is formed. This new structure is joined to the lips of the fenestra all round. In the cephalic part the connection is formed by membrane, while in the caudal part there is more or less continuity between the cartilage of the ear capsule and that of the new operculum. Furthermore, in the cephalic part the lips of the fenestra include the operculum (Fig. 7, p. and op.).

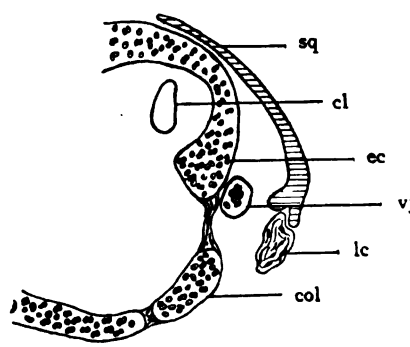

FIG. 1.—Ambystoma punctatum, mature larva 48 mm. long; sq., squamosum; cl., canalis lateralis; ec., ear capsule; vj., vena jugularis; lc., ligamentum squamoso-columellare; col., columella.

(*c*) The columella becomes more firmly united and finally incorporated with the ear capsule.

(*d*) The connection of the columella with the squamosal persists and shifts so as to include the quadrate (Figs. 4-6, sq., col., lc. and q.). There is thus formed a fourth connection of the quadrate with the cranium (Fig. 6, q.).

(*e*) The formation of a bulla-like structure extending backwards (Fig. 7, p.).

(*f*) The establishment of a muscular connection between the operculum and the supraclavicle. This is the m. opercularis described by

Gaupp[11] and Iwanzoff.[12] It is interesting to note at this point that the occurrence of this muscle or its attachment to the sound-transmitting apparatus is not found in such forms as Necturus, Proteus, larval Ambystoma, etc., in which there is a squamoso-columellar connection.

The "bulla-like structure" mentioned above is composed entirely of an outpocketing of the ear capsule, the cavity of which is occupied by an extension of the cavum perilymphaticum. For purposes of the present paper we will speak of this as the perilymphatic prominence,—in accordance with its external form. In the latero-ventral wall of the perilymphatic prominence is a foramen which for the present we desig-

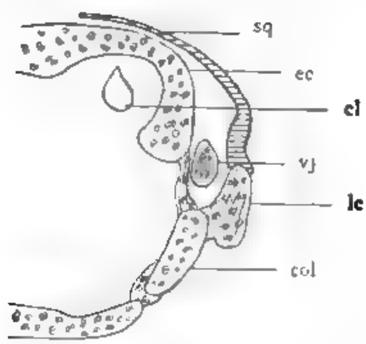

FIG. 2.—Ambystoma punctatum, mature larva, 48 mm. long; section farther caudad; sq., squamosum; cl., canalis lateralis; ec., ear capsule; vj., vena jugularis; lc., ligamentum squamoso-columellare; col., columella.

nate the secondary vestibular foramen in order that we may not confuse it with the primary foramen, of which it is doubtless an extension. This foramen is closed by the above mentioned operculum. This is an entirely new development caudad and ventrad of the columella.

The changes which come about in the sound-transmitting apparatus of Ambystoma at transformation show many striking resemblances to the development of the plectrum and operculum in the frog as described in the excellent monograph by Gaupp. A summarized statement of his results as there given is as follows:

[11]Gaupp, E. Beiträge sur Morphologie des Schädels, I. Primordialcranium und Kieferbogen von Rana fusca. Morphol. Arb., herausgegeben v. G. Schwalbe, Bd. 2, 1893.

[12]Iwanzoff, N. Zur Anatomie der Knöchelchen des Mittel-Ohres d. Amphibien u. Reptilien. Anat. Anz., Bd. IX, 1894.

(*a*) The operculum is developed out of the ear capsule with which it is connected at its caudal end.

(*b*) The columella develops as an independent structure occupying a place cephalad of the operculum and becoming fused with the cephalic margin of the fenestra vestibuli.

(*c*) A part of the crista parotica with which the processus superior columellæ is connected develops from the quadrate.

(*d*) A muscle extending from the supraclavicle has its cephalic insertion upon the operculum (m. opercularis).

From the development in Ambystoma, as well as in the frog, it would appear that there are two distinct structures,—an operculum formed out of the ear capsule, at least in part, and a columella arising independently. This was the original view of Gaupp. We will have occasion to refer to it later in a discussion of the nomenclature of the parts here involved.

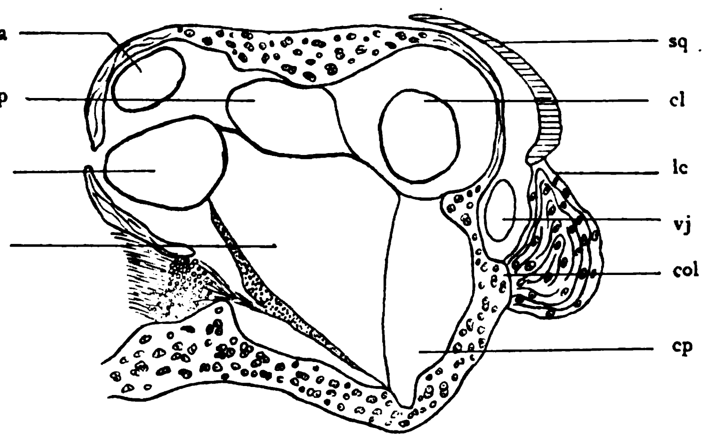

FIG. 3.—Ambystoma punctatum transforming period; ca., canalis anterior; cp., cavum perilymphaticum; u., utriculus; s., sacculus; sq., squamosum; cl., canalis lateralis; lc., ligamentum squamoso-columellare; vj., vena jugularis; col., columella.

That there are two distinct parts that have been variously spoken of as operculum and columella interchangeably is rendered very plausible by a comparison of the relations in other Amphibia.

In Ambystoma, Gyrinophilus and Diemictylus in the adult forms the perilymphatic prominence is well developed, containing, as has been said, an extension of the cavum perilymphaticum, the middle of the

prominence being about opposite the origin of the ductus perilymphaticus. During the larval period in Gyrinophilus the columella has intimate connection with the squamosum, which in this form, as in Spelerpes, Plethodon, Hemidactylum and Desmognathus, is affected by a process of either bone or cartilage, conveniently termed by Gaupp the stylus columellæ. In the adult Gyrinophilus, however, the columella by its stylus becomes more closely connected with the quadrate, as in

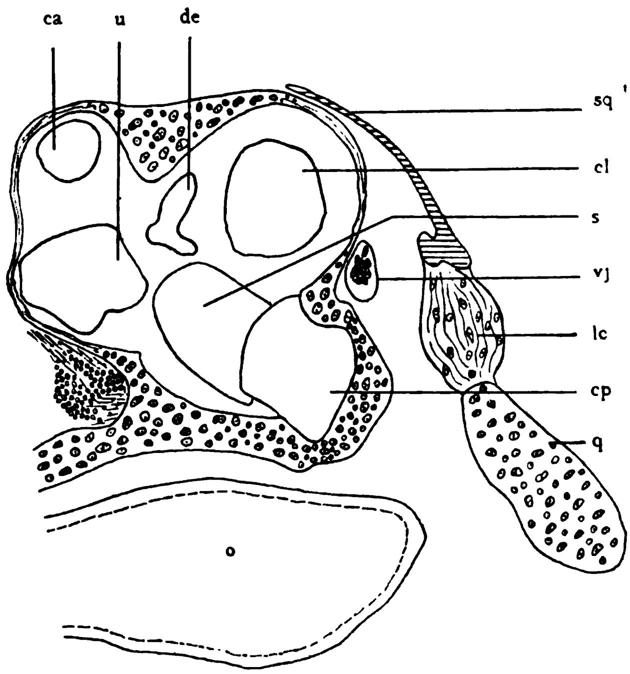

FIG. 4.—Ambystoma punctatum, transformation period; section farther cephalad; ca., canalis anterior; u. utriculus; de., ductus endolymphaticus; sq., squamosum; cl., canalis lateralis; s., sacculus; vj., vena jugularis; lc., ligamentum squamoso-columellare; cp., cavum perilymphaticum; q., quadratum; o., oral cavity.

Ambystoma, although the association is not as intimate as in that form. We are not as yet prepared to state definitely the difference between the larval and adult Gyrinophilus respecting the quadrate and squamosal connections, or what portion of the sound-transmitting apparatus (operculum) of the adult is formed by the columella.

The same peculiar disposition of the operculum, perilymphatic prominence and opercular muscle that is found in the adult Ambystoma and Gyrinophilus occurs also in the transformed Diemictylus. In this last form, although larvæ 19 and 37 mm. in length were examined as well as land forms (which are intermediate between the larva and the adult) and adults, no such squamosal connection of the columella as

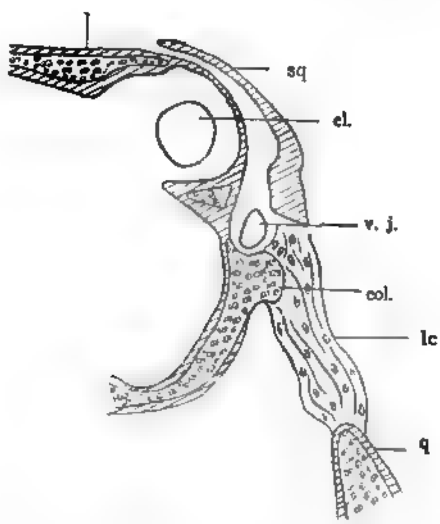

FIG. 5. Ambystoma punctatum, adult 64 mm. long; ec., ear capsule; sq., squamosum; cl., canalis lateralis; vj., vena jugularis; col., columella; lc., ligamentum squamoso-columellare; p., quadratum.

occur in larval Ambystoma, Necturus, etc., was found. No connection between the plate that fills the fenestra vestibuli (operculum), the squamosum and quadrate exists in any of the stages examined by us. In this respect Diemictylus seems to agree with the other members of the family of the Salamandridæ, judging from the works of Parker, Wiedersheim, Stöhr,[13] Fuchs[14] and others. In none of the salamanders examined by them did they find any bony, cartilaginous or ligamentous

[13]Stöhr, F. Zur Entwickelungsgeschichte des Urodelenschädels. Zeitschr. f. Wiss. Zool., Vol. XXXIII, 1879.

[14]Fuchs, H. Ueber die Entwicklung des Operculums der Urodelen und des Distelidiums ("Columella auris") einiger Reptilien. Anat. Anz., Ergänzungsheft z. Vol. XXX, 1907, pp. 8-34.

connection between the opercular apparatus and the squamosum and quadrate. Accepting, as we feel we must, the view that we have to deal here in Amphibia with two structures, it is highly probable that in these closely allied and highly specialized forms the structure designated by us as columella, which is connected with the squamosum, does not come to development or at least disappears early in larval life, either completely or through incorporation with the operculum.

The connection of the columella with the quadrate is not a primary,

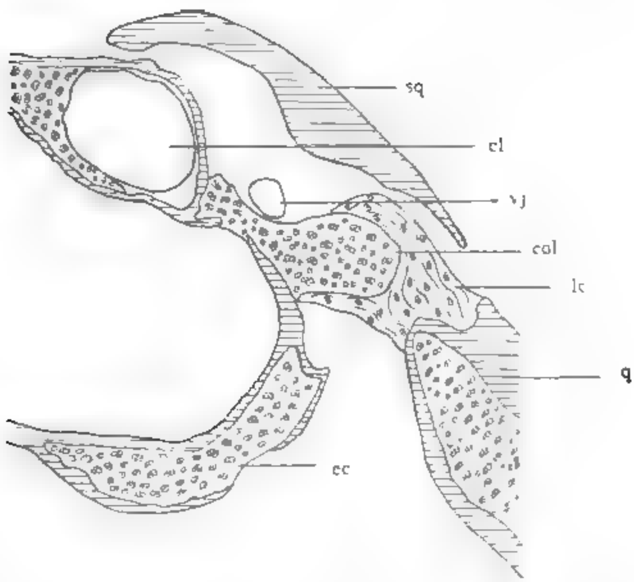

Fig. 6.—Ambystoma punctatum, small adult 100 mm. long; section farther cephalad; sq., squamosum; cl., canalis lateralis; vj., vena jugularis; col., columella; lc., ligamentum squamoso-columellare; q., quadratum; ec., ear capsule.

but a secondary one. This is the connection of the columella with other skeletal structures that is repeatedly emphasized in literature,—a connection with the quadrate. Thus in Amphiuma the stylus columellæ is very intimately connected with a backward-extending process of the quadrate cartilage, the same being true apparently in other forms. In Spelerpes and Desmognathus, larvæ and adult, we find a series of forms in which the conditions in Amphiuma are approached. Likewise in Ambystoma at transformation a close connection is developed between the columella and the quadrate which is absent in the larvæ.

There occur then two connections of the columella with the suspensorium of the lower jaw, one with the squamosum, which is itself closely connected with the quadrate, and one with the quadrate directly, the first being the primary connection both in ontogeny and, we believe, in phylogeny. The view advanced by Gaupp and Drüner that there are two connections of the columella with the quadrate, one above the facial nerve and another below it, has been mentioned at the beginning of this

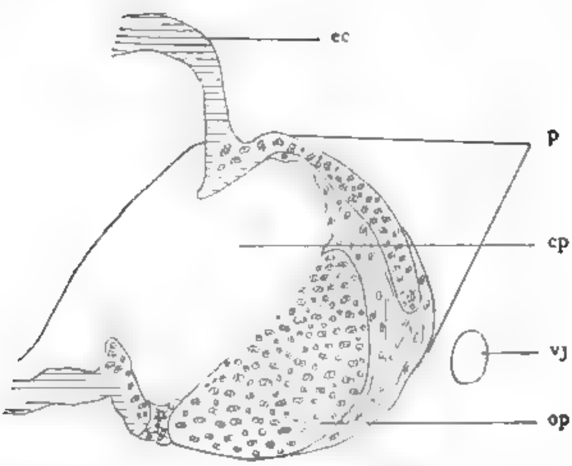

Fig. 7.—Ambystoma punctatum, small adult 100 mm. long; section through caudal part of the operculum; ec., ear capsule; p., perilymphatic prominence; cp., cavum perilymphaticum; vj., vena jugularis; op., operculum.

article. This view is apparently due primarily to the description by Huxley of a connection between the columella and quadrate cartilage in Necturus, above which the facial nerve passes. As it is recognized that this description is erroneous, it is evident that two distinct types of connections of this kind do not exist. In no form known to us does the facial nerve pass above the columellar-squamosal connection with the exception of Necturus and Proteus, in which forms the relations have already been described. In these two forms, as has been previously described by us and others, all the facial nerve passes ventral to (below) the connection in question except the jugular branch, which passes dorsal to (above) it. Since the facial nerve in different forms has often different relations to neighboring structures, as has been pointed out by Drüner and Kingsbury, this different relation in the Proteidæ and in the other Urodeles does not seem to us to offer an obstacle to the

homology of the squamosal columellar connection in these forms with that found in the others. We do not desire to enter further into a discussion of this question here.

As to the homologies of the columella and operculum, we wish here to state merely our belief that the development of the columella independently of the ear capsule as described in Necturus and Ambystoma, together with the very early connection with the bone which we regard as squamosum supports the view of its homology with the hyomandibular-symplectic of fishes, and that the element which we have designated as operculum, as distinguished from the columella, seems to arise from a differentiated portion of the ear capsule itself.

The question of nomenclature of the parts involved needs a word of comment. Gaupp in the frog described the columella and operculum as distinct structures. He has since modified his use of the terms to fit the change of view with regard to homologies and has employed the term columella as a name for the sound-transmitting apparatus of Amphibia, composed in Anura of an operculum and plectron, in Urodela of an operculum and stylus columellæ. In view of the relations described above, it would seem necessary to recognize, in the Urodeles at least, two distinct structures, which may be termed respectively columella and operculum, the first arising independently and connected primarily with the squamosum and in some forms secondarily with the quadrate cartilage, the second, the operculum, having no such connection and developed largely at least out of the ear capsule.

The Columella Auris in Amphibia

B. F. KINGSBURY and H. D. REED

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THE COLUMELLA AURIS IN AMPHIBIA.

Second Contribution.

B. F. KINGSBURY AND H. D. REED.

Table of Contents.

In 1908 the authors published a partial report[1] upon the morphological relations of the so-called Sound-transmitting Apparatus in representative Urodeles with a view to establishing the type or types

[1]Anatomical Record, Vol. II, No. 3, June, 1908, pp. 81-91.

and their modifications. In this study the following possible general aspects were kept in mind: (1) The primary (primitive) and secondary character of the connections and relations of the structures occupying the *fenestra vestibuli* more generally designated as constituting the Columella auris, (2) comparison with the forms below (fishes) the amphibian group (the hyomandibular homology), (3) homology with the reptilian Columella and mammalian Ossicula auditus, (4) the comparison and homology in Urodela and Anura, (5) the relationships of the different urodele families, (6) the function and functional importance of these structures in the tailed amphibia, (7) the variation in the arrangement of the parts of the apparatus and its significance.

It is not necessary to repeat here the reasons that led us to believe an extensive re-examination of the comparative morphology of the structures fitting into the *fenestra vestibuli* in urodeles to be necessary, as they were briefly set forth in the first paper and previously by others (Gaupp, '98; Drüner, '03). In the examination of the different forms, there have been kept in mind the following morphological relationships:

1. Relation (connection by fusion, articulation or ligament) of the Columella (stilus columellæ) to
   (*a*) the os. squamosum (paraquadratum, Gaupp),
   (*b*) os. quadratum or palatoquadratum,
   (*c*) hyoid (ceratohyale);
2. Relation to the carotid artery (*Arteria carotis interna*) and jugular vein (*Vena petroso-lateralis*);
3. Relation to the otic capsule (lips of the *fenestra vestibuli*);
4. Relation to facial nerve (*ramus hyomandibularis* VII);
5. The ligaments coming into relation with the parts involved,—
   (*a*) *Ligamentum squamoso-columellare*,
   (*b*) *Ligamentum hyo-suspensoriale*,
   (*c*) *Ligamentum hyo-mandibulare*,
   (*d*) *Ligamentum hyo-columellare;*
6. *Musculus opercularis.*

Since early in the investigation it became apparent that there were two morphologically distinct elements appearing in the different forms, comparable, at least, if not homologous (*vide subseq.*) as we believe with the plectrum (columella) and operculum in the frog. it

became necessary to keep in mind the development of each element in its relation to the ear capsule. In the present paper a *detailed* presentation of the developmental changes, even as far as they have been worked out, is not included.

In addition to the forms briefly described in the first publication made by us, there have been examined by means of serial sections through the head, 14 species representing 1 family and 12 genera. The total number comprises 8 families, 21 genera, and 23 species, in the case of all save 9 of which the structure and morphology in both larvæ and adults were investigated. Bearing in mind that the total number of the families and genera of tailed amphibia is 8 and 45 respectively, it may be seen that a comprehensive and at the same time detailed view has been gained of the relations of the urodele "sound-transmitting" apparatus.

Without entering upon a full discussion of the bearing of our investigation, which is reserved for the last portion of this paper, the more important results may be stated briefly at this point.

1. In the tailed Amphibia, there may be developed two separate fenestral elements fitting into the *fenestra vestibuli.* These have been termed by us *Columella* and *Operculum* respectively.

2. The *Columella* typically possesses a *Stilus* which is connected primarily with the ventral (or ventro-caudal) edge of the squamosum. The *Stilus columellæ* may secondarily become joined to the palatoquadrate.

3. In development its proton appears outside the otic capsule as a group of cells continuous with the cells between the otic process of the palatoquadrate, squamosum and ear capsule.

4. The facial nerve in the forms examined is entirely below (and in front of) the columella save in Necturus, Proteus and Typhlomolge, in which the *Ramus jugularis VII* passes above the squamoso-columellar connection.

5. The *Operculum* is developed out of the otic capsule. Its position relative to the columella is caudal and medial. It possesses no skeletal connections but gives attachment to the *M. opercularis.*

6. In one group of forms, the columella only is present. In the Ambystomidæ the columella is present during the larval period but

becomes fused with the ear capsule at transformation when an operculum is formed. A further reduction and fusion of the columella is encountered in Salamandra, Triton and Diemictylus (Salamandridæ and Pleurodelidæ, Cope). In the Plethodontidæ and Desmognathidæ the fenestral plate of the columella embodies a representative of the operculum which is not separately developed.

7. The hyomandibular homology of the Columella is strengthened.

How widely the results of a detailed examination of a large number of forms depart from the interpretations at present accepted based upon the available information as to the morphology in a more limited number of salamanders, may be seen from a comparison of the above with the statements in two of the standard works: The Comparative Anatomy of Vertebrates, by Dr. Robert Wiedersheim, and the section upon the development of the skull, by Dr. Ernst Gaupp, in Hertwig's Handbuch der Entwickelungsgeschichte der Wirbeltiere.

The former ('06) describes[2] the *fenestra vestibuli* as filled by a cartilaginous plate, the so-called *Stapedial plate* or *Operculum* which is joined to the Palatoquadrate and Paraquadrate (squamosum) by ligaments, cartilage or bone. This bridge between the stapedial plate and the quadrate (or paraquadrate) is called *Columella* and together with the *Operculum,* in a phylogenetic sense, corresponds with the proximal segment of the hyoid arch (hyomandibulare or possibly symplecticum). Ontogenetically such a relation does not occur, both operculum and columella arising by differentiation in the territory of the otic capsule.

Professor Gaupp ('05) in Hertwig's Handbuch (pp. 696, 697, 605) designates the entire "stapedial" element as *Columella auris,*

[2]"Sie [Fenestra ovalis] wird von einem durch Bandmassen oder auch durch Knorpel oder Knochen an das Quadratum und Paraquadratum befestigten Knorpeldeckel, der sog, *Stapesplatte* (St) oder dem *Operculum*, verschlossen und soll uns bei der Anatomie des Gehör-Organs wieder beschäftigen. Jene zwischen Stapesplatte und Quadratum resp. Paraquadratum sich erstreckende Brücke heisst *Columella* und entspricht zusamt dem Operculum in phylogenetischer Beziehung dem oberen Abschnitt des *Hyoidbogens*. Ontogenetisch ist von diesen Beziehungen nichts mehr nachzuweisen, sondern es handelt sich sowohl für die Columella als für das Operculum hinsichtlich ihrer Entstehung um Differenzierungsprocesse im Bereich der Labyrinthkapsel."

consisting of an *Operculum* which may or may not bear a process, the *Stilus columellæ*. The process when present is usually connected by means of a ligament (Ligamentum suspensorio-columellare) with the Paraquadratum, Palatoquadratum or with both. The facial nerve in most forms passes below the suspensorio-columellar connection. It is stated, however, that there are two such connections, one above and one below the facial nerve. The operculum with a stilus is regarded as the more primitive condition and as such is probably to be homologized with the Hyomandibulare. In the Anura the Columella auris consists of two elements, *Operculum* and *Plectrum,* the latter (*Pars interna plectri*) probably to be interpreted as a stilus which has become secondarily dissociated from the operculum.

Nomenclature. The question of nomenclature is a perplexing one. Gaupp has termed the entire fenestral structure, Columella auris, consisting in Anura of two elements, Operculum and Plectrum, in Urodela of Operculum and (typically) its process, Stilus Columellæ. The direct application of the terms used by Gaupp, though desirable, becomes difficult in the light of the existence of a stilus-bearing fenestral plate and a non-stilus-bearing fenestral plate in the same form and at the same time. While there are objections to both the terms *Columella* and *Operculum,* it seemed better to avoid the introduction of new terms and to employ the term *Operculum* for the *stilus-free* structure and to restrict the name *Columella* to the *stilus-bearing* element. This use of terms seems to necessitate less departure from the earlier use of the names. The operculum of Anura is directly comparable with that which is termed by us operculum in the Urodela. This in Siredon was termed *Operculum cartilageneum* by Windischmann in 1831 and subsequently has often been designated Operculum in other salamanders. Columella was, of course, applied to the anuran structure now named *Plectrum* by Gaupp, and to the stilus in Urodeles, or to the entire element (Hasse, '73) called columella by us.

As an indifferent name for bony or cartilaginous plate fitting into the *fenestra vestibuli* we employ the term *fenestral plate.* A backward extension of the *Cavum perilymphaticum* beneath the operculum we designate *Recessus perilymphaticus.* For the bulging por-

tion of the ear capsule associated with the outpocketing of the perilymphatic space we employ the name *Prominentia perilymphatica.* Without going into a discussion of homologies, we designate as Os squamosum the Os paraquadratum of Gaupp, but in the use of other names we adhere to the terms used by him. The term *proton* is used as the equivalent of the German word *Anlage.*

We depart from the usages of the preliminary paper[3] in substituting *Vena petroso-lateralis* for *Vena jugularis interna* of which it is a direct continuation, employing the name used by Drüner, likewise using his term, *Musculus cephalo-dorso-mandibularis* for *Muscularis depressor mandibuli. Palatoquadratum* is substituted for *Quadratum.*

Acknowledgments. We have received material for study and helpful criticism from many sources and wish especially to express our indebtedness to Professors Wilder and Gage and Dr. W. A. Hilton of Cornell University, Professor Robert Wiedersheim of the University of Freiburg and Mr. B. G. Smith of Syracuse University. Aside from personal obligations we wish to express our appreciation of the works of Wiedersheim and Gaupp in this field of research.

AMBYSTOMIDAE.

Ambystoma[1] *punctatum.* Two reasons determined the choice of this form as one of the species in which to work out quite thoroughly the development of the ear region: (a) the ease with which a large number of stages, larval, transforming and adult, could be procured; (b) its systematic rank as a typical urodele. In all, some forty series were examined and four models prepared. In this way was obtained a complete history of the transformations through which

[3]*Errata.* At this point we desire to correct errors that were allowed to creep into manuscript and proof in the earlier paper:

(1) p. 83, line 2, Hemidactylum should read Hemidactylium.
(2) p. 83, line 11, 4-6 mm. should read 12-14 mm.
(3) p. 83, line 17, 1888 should read 1879.
(4) p. 86, line 2, caudal should read dorso-caudal.
(5) p. 87, line 4, Hemidactylum should read Hemidactylium.
(6) p. 87, Fig. 4, D.e. should read D.p.—Ductus perilymphaticus.

[1]The same as Ambystoma according to older usage.

the structures under consideration pass. The results of the study in this species were given in concise form in our first or preliminary paper. The evidence upon which the conclusions were based was not submitted at that time, however, and may be given now, together with such further details as are important in this connection.

The first definite trace of the columella is to be found in embryos of 11-13 mm. in length, a short time before hatching. At this period while the cupola of the otic capsule is chondrified, the basal plate is still in the pre-cartilage (chondroblastema) stage so that the ventral boundary of the primary fenestra is not yet sharply defined, and the difficulty of delimiting its ventro-medial side is further increased by the fact that the cells of the future floor as well as those occupying the site of the future membrane are equally rich in yolk granules, in which respect they differ from the cells of the surrounding mesenchyma. The squamosum is just appearing as a minute scale of bone above and behind the otic process of the palatoquadrate.

Below and beneath the squamosum, filling in the space between otic capsule, squamosum and otic process of the palatoquadrate, and extending down upon the outer side of the vena petroso-lateralis to the yolk-bearing cells occupying the site of the future membrane, is a dense tissue, with numerous cells and homogeneous matrix, which embodies the proton of the columella, stilus and squamoso-columellar ligament. The derivation of these cells was not definitely determined. Younger embryos lend some support to the view that they migrate down around the vein. The different appearance of the cells of the otic capsule adjoining the lower end of this cell-group argues against their origin from this portion of the otic capsule (membrane or floor).

In a 13-14 mm. specimen the demarcation of the columellar tissue is sharper and the portion against the fenestral membrane denser. The condition at this stage is reproduced in a photograph, Fig. 39, Pl. IV, *col.* At about this time, chondrification begins and in the larva 14-15 mm. in length there is a small cone of cartilage, whose base is against the membrane and whose apex projects out into the dense tissue still connecting with the cell-group between squa-

mosum, otic capsule and otic process of the palatoquadrate. The stilus appears to chondrify out into this tissue, the unchondrified portion of which becomes the Lig. squamoso-columellare.

The development as given above agrees completely with the concise description of Killian ('90) for the development in Siredon. He terms the columella *Operculum* and had no knowledge of the interesting changes occurring at transformation.

During the period of larval growth the portion of the columella fitting into the membrane increases greatly in size, becoming an elongated plate of cartilage which for purposes of convenient reference may be designated *Fenestral Plate.* If at first it is outside the fenestral tissue, it becomes in the process of growth a part of that structure. Whether the enlargement of the plate takes place through marginal growth with the incorporation of fenestral tissue, or through interstitial growth with a simple displacement of the bordering membrane, has not yet been determined. In late larval life the columella apparently becomes joined to the dorso-cephalic margin of the fenestra by delicate cartilage and subsequently more closely connected with the ventro-cephalic edge. Ossification appears late. Two plates of bone are formed, one upon the inner surface of the columella, the other upon its outer surface also extends out upon the stilus. This method of ossification of the columella is quite characteristic for other urodeles as well. Fig. 33 (Pl. III) illustrates the development attained by a 35 mm. larva.

The condition shortly before transformation is shown in Fig. 22 (Plate I), from the model of the ear region in an individual about 45 mm. long. The fenestra vestibuli (*F. v.*) whose complete outline cannot of course be seen from the figure, is an elongated oval whose dorsal border is formed by the crest of cartilage where the lamina horizontalis of the lateral semicircular canal passes into the lateral wall. For purposes of reference we shall refer to this as the Crista semicircularis (Cr. s.). At the cephalic end of the fenestra the "lips" join to form an elongated prominence with which the processus basalis palatoquadrati articulates. Its interior is occupied by a cephalic extension of the cavum perilymphaticum. The caudal end of the fenestra attains nearly the end of the caudal

cupola of the otic capsule. It may be noted that the fenestra vestibuli is in the lateral wall of the ear capsule, becoming more ventral in its cephalic portion.

The fenestral plate occupies the larger portion of the window, being most widely separated from the margin of the fenestra at its caudal end. In the model the relations of the arteria carotis interna and vena petroso-lateralis are shown crossing and partially covering the fenestral plate. In Fig. 23 (Plate I), however, in a somewhat later stage, the complete outline of the fenestral plate can be seen. At the cephalic end, on both ventral and dorsal margins, new cartilage, not shown in the model, is just beginning to join the columella to the margin of the fenestra vestibuli. The stilus and ligament connect the fenestral plate with the ventral edge of the squamosum. The palatoquadrate cartilage does not become connected with the ligament. A blunt process of the quadrate underlying the squamosum is not brought into relation with the ligament at this stage.

At transformation the fenestral plate becomes joined to the lips of the opening on all sides save the caudal and the caudal portion of the ventral side. There is, however, a portion of the primary fenestra behind the stilus where even in the fully grown salamander the wall of the otic capsule is very thin,—membranous or filled in with a thin lamina of cartilage (See Fig. 24, Pl. I, "F"). In Fig. 23 the outlines of the old fenestral plate still shows. The delicate new cartilage just forming was not modeled. In Fig. 24, the fusion of the plate with the edge of the fenestra is nearly complete. The outline of the old columella and the newly formed cartilage can be distinguished.

In the process of transformation, due to the shifting of the suspensorium, the attachment of the stilus becomes largely transferred from the squamosum to the palatoquadrate cartilage (Pl. I, Fig. 24).

The operculum present in the transformed salamander (Pl. I, Fig. 24, *Op.;* Pl. II, Fig. 25) occupies the caudal portion of the new fenestra (definitiva) whose dorso-cephalic margin includes the cephalic end of the operculum; the caudal end projects freely and to it is attached the M. opercularis whose tendon fits into and fills a depression upon its external surface (Pl. IV, Fig. 35).

The operculum is formed out of the wall of the ear capsule upon the medial side of the caudal portion of the fenestra. Fig. 23 shows the operculum in process of formation. Along the line marking the medial border of the new fenestra the cartilage breaks down and is absorbed, cutting out in this way a large plate from the ventral wall near the caudal end of the ear capsule. In this histolysis, while the end result is a backward and medial extension of the fenestral opening, it is not accomplished by an actual extension back of the fenestra, but the cartilage is absorbed all along the line of separation, several irregular clefts appearing first which afterwards become confluent with each other and with the fenestra. At its caudal end the separation of the operculum comes later and at this point a new formation of cartilage occurs extending the operculum in that direc-

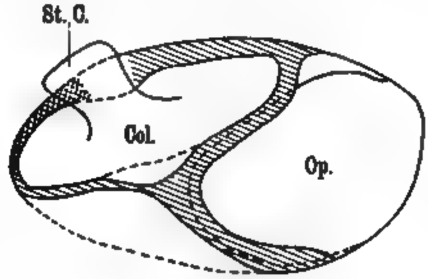


FIG. 1. Schema illustrating the fusion of the columella with the ear capsule.

tion outside the ear capsule. New cartilage is, however, formed at the edge of the fenestra as well and in the operculum itself which attains massive dimensions in the fully grown Ambystoma (Pl. IV, Fig. 35).

The inclusion of the cephalic end of the operculum by the lips of the fenestra (Pl. I, Fig. 24) is accomplished by a deposit of new cartilage which cements in solidly the fenestral plate and extends the fenestral lip backward outside the operculum. The dorso-cephalic portion of the margin is thus formed by the ventral and caudal edges of the larval columella extended by new cartilage formation, while the ventro-cephalic margin is new cartilage formed upon the ventral lip of the primary fenestra which extends to meet that deposited on the fenestral plate. The diagram, Fig. 1, will

illustrate the transformation and the filling in of the primary fenestra and the incorporation of the fenestral plate. The columella, stilus columellæ, and operculum are indicated by *Col.*, *St. C.*, and *Op.* respectively; the new cartilage is line-shaded, while the region of earliest fusion is cross-hatched. The outline of the included portion of the operculum is marked by a broken line.

In the larva approaching transformation (Fig. 22, Pl. I), the operculum is not well outlined, although a slight groove causes a prominence of the wall which later becomes the operculum. As shown in Fig. 31 (Pl. III), in the sections of the ear-capsule of mature larvæ, the region from which the operculum will form, may be recognized. Compare Figs. 31 and 32, in the latter of which the histolysis of the thin cartilage on the medial side of the future operculum is severing its continuity with the remainder of the floor of the otic capsule. The operculum thus arises from a portion of the floor of the ear capsule while the secondary fenestra with the plate of the columella is in the lateral wall. (Cf. Figs. 32 and 33.)

The interior of the ear capsule, opposite the region to become the operculum, is occupied by the cavum perilymphaticum (Figs. 31 and 32, Pl. III). In the transformed animal this portion of the ear capsule becomes somewhat prominent and may be termed the Perilymphatic Prominence (*Prominentia perilymphatica*) (Figs. 30 and 35). The outward and backward extension of the perilymphatic space on the inner side of the operculum, as stated above, is termed *Recessus perilymphaticus*.

The muscle attaching to the operculum to which Gaupp ('93) gave the name of *M. opercularis*[5] extends caudad and at its caudal end is attached to the outer side of the *Suprascapula*. In the larval Ambystoma it is not present. Early in the transformation myoblasts upon the outer edge of the ventral spinal musculature (M.

[5]This muscle in the frog was regarded as a portion of the "Occipito-subscapularis" by Dugès ('35), the Levator anguli scapulæ of Ecker. Cope ('88 a and b) has termed it M. stapedius, Iwanzoff, M. protrahens scapulæ. Gaupp subsequently ('96) designated it the "Pars opercularis of the M. Levator scapulæ superior." In Urodela it seems to deserve recognition as a distinct muscle, and its development apparently differs somewhat in the two groups.

intertransversarius capitis inferior of the frog, Gaupp, '96) develop into a fascicle of small fibers which becomes separated off from the above mentioned muscle and gains the attachments to the developing operculum and the suprascapula. Its opercular attachment is shown in the models pictured in Figs. 23 and 24 (Pl. I) and also in Fig. 37 (Pl. IV) in which both attachments are shown.

In accord with the statement of Hasse ('73), the facial nerve is entirely below (in front of) the columellar-squamosal connection, the descriptions of other authors who have given its relations being therefore incorrect. In Fig. 22, the three branches of the hyomandibular division, ramus mandibularis internus, ramus mandibularis externus, and ramus jugularis, are shown. Joining the R. jugularis is the R. communicans IX (not shown) which pursues a course dorsad to the carotid artery to join the R. jugularis where it passes under the ligament.

In Ambystoma, therefore, there are two fenestral structures which succeed one another at transformation. The first which appears in the larva, is the columella, whose stilus connects with the squamosum and whose fenestral plate becomes associated with the otic capsule at its cephalic end. At transformation the columella becomes fused with the ear capsule and a second fenestral plate, the Operculum, is cut out. This second structure is caudal and medial to the first, possesses no process (stilus), is not connected with the squamosum or palatoquadrate, but is joined by means of the M. opercularis to the pectoral girdle.

The examination by earlier workers of the otic region in Ambystoma or Siredon,—which is to be regarded as a permanent larva of an Ambystoma,—has not lacked suggestion of the interesting condition found in this form. In Siredon, in which the condition has usually been examined, Hasse ('73), Friedenreich and Gegenbaur ('49), as well as Wiedersheim ('77), Parker ('77), and Retzius ('81), described a well ossified "operculum" of conical form, the base of the cone fitting into the fenestra, the apex of the cone prolonged into a bony process attached to the palatoquadrate cartilage by ligament (Gaupp, '99, p. 1040). The plate that fits into the window possesses, according to Retzius, a cartilaginous border and

the tip of the stilus is likewise of cartilage. This description of the condition in Siredon corresponds fairly well with the relations of the columella in Ambystoma before transformation. The names applied to the structure varied: Operculum (Wiedersheim); Columella (Hasse); Stapes (Parker). Windischmann ('31), whose paper we have not been able to examine, described in Siredon a stilus whose (fenestral) plate he termed *Patina,* while behind the *Patina* there was an *Operculum cartilagineum* joined with it only by connective tissue. This description of Windischmann's was discredited by later workers. It is probable, however, in view of the possibility that many, perhaps most, of the so-called Siredons were larval Ambystomas and not super-larvæ (Axolotl) that Windischmann correctly described the condition in a transforming individual. More recently Iwanzoff ('94) describes the condition in Siredon as follows, apparently erring in ascribing the connection of the columella with the squamosum to the operculum:

"Bei Siredon befestigt sich der Musculus protrahens scapulæ mit seinem proximalen Ende am rundlichen Knorpel auf der hinteren Wand des Schädels. Parker und Wiedersheim halten diesen Knorpel einfach für einen Teil des Knorpelschädels, um so mehr, da er schwach von dem letzteren abgegrenzt ist. Aus dem nachgewiesenen Grunde nehme ich ihn für den Stapes, um so mehr, als er demselben auch nach seiner Lage entspricht. Desshalb ist der Teil, welchen die genannten Autoren als Stapes annehmen, nämlich die teils knöcherne, teils knorpelige und bindegewebige Bildung, die vom Stapes zum Quadratknorpel und Squamosum, und dieselbe Lage, wie das Band mit den Columellarknöchelchen bei Pelobates hat, für die Columella zu halten. Auf diese Weise erscheint die gewöhnliche Behauptung, dass bei den Urodelen die Columella gar nicht existirt, für Siredon und einige andere Formen, irrthümlich."

Iwanzoff seems, therefore, to have seen two structures, though their detailed relations were confused. The early description of Windischmann portrays most closely the condition in Ambystoma, though all the descriptions were doubtless approximately correct if the age (larval or adult) is considered. *No one seems to have recognized the fact that the condition changes with age.*

Turning now to the development of the "sound-transmitting" apparatus in Ambystoma, we find that only imperfect glimpses of the true development were obtained, and it is not always easy to determine to which structure they refer. Wiedersheim, Parker, Stöhr, Killian, Witebsky, Winslow, have examined one or more stages in the larval Ambystoma or Siredon (Axolotl). Wiedersheim and Winslow evidently described the development of the columella; Witebsky saw the independent chondrification of the columella but missed the connection of the stilus with the squamosum (or palatoquadrate) and drew from his observations some quite irrelevant conclusions as to the homology of the columella for which he had no sufficient basis in fact, as has been pointed out by Gaupp ('98) from whose paper our information is gained, Witebsky's dissertation being inaccessible to us here. Stöhr made his examination of the development in the Axolotl only incidental to a more detailed study of the development in Triton, so that he simply "confirmed" the results of Parker's more extended investigation, stating that the "operculum" grows out of the cartilaginous border of the fenestra vestibuli. He gives no figures, so that it is difficult to interpret his results. It was apparently the *Columella* (our use) that he had under observation. Parker alone examined an extended series of larval Ambystoma (Axolotl, Siredon) including an adult Ambystoma. For the first seven stages neither his words nor his figures give indubitable proof that he saw the development of the columella or recognized the stilus or its connection. His description (p. 564) of the adult (Ambystoma opacum) indicates that in his stapes he described the operculum.[6] In two points there was probably mistaken identification; ligament and ossification were doubtless absent. The descriptions of two large Axolotls (8½ and 8¼ inches long) undoubtedly applied to the Columella,[7] the recognition of the suspensorial connection above the facial nerve being noteworthy.

[6]"The bulging bony floor of the vestibule forms a widely crescentic bulla, and in the notch the fenestra ovalis contains a small lenticular stapes, the center only of which is ossified. The spiracular ligament fastens the stapes to the back of the top of the suspensorium."

[7]Page 559. "the stapes (Figs. 2, 4 and 5, st.) is unusually solid and projecting, its outstanding process looking a little forward. From that process

Winslow ('98), on the other hand, has described and figured models of three stages of the chondrocranium of Ambystoma. He describes the columella (Stapes) chondrifying as an independent center in a 12 mm. individual. The condition in a 37 mm. larva he describes as follows: "The fenestra ovalis is now nearly filled by the stapes (s), which has a slight prominence directed outwards and upwards from the antero-dorsal angle of the cartilage towards the otic process of the quadrate. These cartilages, however, do not become united at any time during the development of Ambystoma as they do in some other forms." In a young adult, 69 mm. in length, he describes the stapes as in the posterior portion of the fenestra closely applied against the remnant of the cartilaginous wall of the capsule, this time describing the operculum as stapes. His figure bears out the brief description and shows the stilus of the fused columella extending from the ear capsule to the palatoquadrate.

It is hardly necessary to comment on the difficulties of interpretation in such a form as Ambystoma if the changes at transformation are ignored. Transformation occurs relatively quickly and at this time the salamanders are less easily procured.

Chondrotus tenebrosus. Three examples of this species were examined; larval, transforming, and adult. It was not surprising to find that the relations in this salamander closely resembled those in Ambystoma because of the close relationships of the two genera.

The larva was well advanced (58 mm. long) and the morphological relations diagrammatic in their clearness. The otic capsule as also the remainder of the chondrocranium is unusually heavy, and the columella shares this characteristic. As shown in Fig. 34 (Pl. III) there is a well developed stilus which articulates closely with the lower edge of the squamosum. In no other form examined by us has a single section shown the distal connection as well as the central origin of the stilus from the fenestral plate, as a result of

a ligament arises which spreads into a fan-like fascia, which is inserted along the under and outer edges of the suspensorium from the lobe of the otic process to the lobe of the quadrate . . . it lies some height above the portio dura. . . ." Page 562. "Thus we have here what may be called a *spiracular fascia*, the counterpart of the spiracular cartilage and bone of the Menopome and others."

its more transverse course, since in Ambystoma as well as the other forms examined it has a course outward, upward and also forward (See, however, Siren, p. 598). The fenestral plate is at no point connected with the otic capsule, at the edge of the fenestra or elsewhere. A few sections farther forward the distal end of the stilus is joined by connective tissue with the caudal edge of the palatoquadrate, this junction not being as close, however, as that with the squamosum. The relations of artery, vein and facial nerve are as in Ambystoma (Pl. III, Fig. 34).

The second specimen was well along in transformation (150 mm. long, gills mere stumps). At this stage the columella is connected by membrane with the lips of the fenestra everywhere save on its cephalo-ventral border where cartilaginous fusion has begun. Its stilus is massive and abuts against the palatoquadrate with which it is joined by connective tissue (Pl. IV, Fig. 36, St. C.). The *Os. pterygoideum* also comes into close relation with it, but the connection with the squamosum existing in the larva is now much less direct (Fig. 36). The characteristic inner and outer ossifications are present, with accompanying changes in the cartilage.

The floor of the ear capsule medial to the caudal portion of the fenestra is nearly completely cut out as the operculum (Pl. IV, Fig. 38, *Op*). In its present development, it may be compared with the stage in Ambystoma shown in Fig. 32 (Pl. III). An opercular muscle attaches to the operculum. The recessus perilymphaticus is characteristically present.

The adult individual was 240 mm. long and was examined by dissection. The condition found was much like that in the adult Ambystoma. The columella, with its inner and outer bony surfaces, the latter bearing a well ossified stilus, is completely fused with the otic capsule forming the anterior boundary of the nearly circular fenestra into which was fitted a cartilaginous operculum, roughly hemispherical in form, its flattened surface bearing a tendon, doubtless that of the M. opercularis, which was not, however, dissected out. Fusion with the otic capsule was apparently by cartilage only, so that, by the use of some force, the stilus and plate could be and were completely broken away. The distal end of the stilus was con-

nected by syndesmosis with the under surface of the squamosal near its caudal edge, and doubtless also with the palatoquadrate cartilage as well, though this relation was not determined.

Examination of the condition in the adult of this salamander by means of dissection was made partly because other adult members of this family had been examined in this way. Of three Asiatic genera, Hynobius (Ellipsoglossa nævius) Salamandrella (kaiserlingi), and Ranidens (Randon sibericus) the "operculum" (columella) is described by Wiedersheim, '77, (503, 519) as a remarkably large cone of bone whose columella [stilus columellæ] is closely joined to the lower end of the quadrate. As a result of this intimate connection Wiedersheim called attention to the inevitable shaking of the perilymph that must attend every violent closing of the jaw,—as in the seizing of prey,—an arrangement whose physiological significance it is difficult to comprehend. Granting, however, that as in Ambystoma and Chondrotus, the columellar plate is fused with the ear capsule, the difficulty found in the close junction of stilus and palatoquadrate disappears, a fused element not being subject to violent agitation from movement of the jaw, but on the contrary offering a firmer support for the upper end of the quadrate.

The suggestion is, therefore, made that the columella will be found fused in the other Ambystomidæ, including these Asiatic forms, and it is not without some direct evidence. Fig. 65 in Wiedersheim's monograph ('77) shows the stilus in Ellipsoglossa (Hynobius) arising, not from the opercular plate, but from the anterior lip of the fenestra, as in Salamandra. This is also just as he figures it in Ambystoma Weismanni (tigrinum) ('79, Fig. 8),—quite different, as might be expected, from the relations in the Axolotl ('79, Fig. 12). The operculum had been removed. His ('77) Fig. 67 (Ranidens), however, suggests a condition such as is found in Cryptobranchus.

Okajima ('08) has recently given a short description of the columella in another member of the family,—Onychodactylus japonicus. An ossified plate, "hollow" in the center with cartilaginous border, he states (p. 353, 354) fits into a lateral fenestra vestibuli. A cartilaginous stilus is connected with the cartilaginous portion of the

quadrate. This is evidently the columella; an operculum was not recognized. A text figure of a section through the ear capsule recalls strongly the similar section in just transformed Chondrotus (Pl. IV, Fig. 38), already described.

Salamandra.

Salamandra maculosa has proved to be a form of rather unusual interest with regard to its sound-transmitting apparatus both in respect to the elements present and their relations when considered in the light of conditions in other forms.

The skeletal elements of the head of Salamandra are quite fully ossified. The os quadratum is composed of a thin outer shell of bone very closely associated with the under surface of the superimposed squamosum. Underneath the os quadratum is the palatoquadrate which is continued into the basal, otic and trabecular (ascending) processes. As has been pointed out by Wiedersheim ('77), the inclination of the supensorium to the long axis of the skull is almost transverse, a condition not met with in many salamanders. The inclination of these elements, whatever its cause, undoubtedly influences the nature of the suspensorio-columellar connection in all forms.

Both columella and operculum are present in the adult. The columella is a plate of partly calcified cartilage fused with the lips of the fenestra vestibuli except in the caudal third of its circumference where it forms the cephalic margin of the definitive fenestra. Fig. 40 (Pl. V) is a photograph of a section through the cephalic portion of the columella and shows how completely it is fused with the ear capsule in this region. In the same figure is shown the short and thick stilus which projects from the dorso-lateral aspect of the columella. It is composed of hyalin cartilage distally continuous with the cartilage of the palatoquadrate; proximally it passes over into the plate of the columella whose cartilage, calcified where it joins the ear capsule, may also be seen in this figure. To the squamosum it is joined by connective tissue representing a short ligament. Describing the "stapes" in Salamandra, Parker ('82a) observes:—(pp. 174-5) "There is a well ossified lip, like the mouth of a pitcher,

to the fenestra ovalis: it looks outwards and backwards; the thick, oval closely fitting stapes (operculum) remains cartilaginous and is only attached to the supensorium by ligaments." In a foot-note he adds: "Mr. A. Doran has shown me a stapes, said to belong to this species, which is ossified and has a stalk. I find nothing of the kind in the specimen dissected by me; and I think it probable that that specimen (in the Hunterian museum) belonged to another kind." It is quite likely that Mr. Doran was correct and that the stilus had by some accident been torn from Parker's specimen. The relation of the stilus to the artery, vein and facial nerve is typical.

The operculum occupies the typical position below and behind the columella filling the definitive fenestra vestibuli. It is a relatively large hemispherical mass of cartilage free all round, attached to the lips of the fenestra by membrane only. The cephalic fourth is overlapped by the caudal margin of the columella precisely as in Ambystoma. This is made clearer by an examination of Fig. 41 (Pl. V), a photograph showing the operculum internal to an overhanging lip of cartilage, the columella, which conceals the entire cephalic and a portion of the dorsal margin of the operculum. In tracing it forward, it gradually diminishes and finally disappears in the middle region of the perilymphatic prominence. The photograph reproduced in Fig. 42 (Pl. V) is of a section in this region, and shows a small lip of cartilage, a backward continuation of the columella, projecting from the ear capsule upon the dorsal margin of the fenestra. Fig. 65 (Pl. X) is a schematic representation of the position and relations of the columella and operculum as viewed from the side.

The perilymphatic prominence is pronounced. To the caudal surface of the operculum is attached the strong M. opercularis which extends caudad to the suprascapula.

Wiedersheim ('77, p. 504), in commenting upon the columella in Salamandra, says: "It is cartilaginous throughout life and rests suspended by the connective tissue in the foramen ovale which is bordered by two thick, crest-like lips. These lips now pass forward and outward in a thin cartilaginous process and this joins the quadrate cartilage,—a remarkable variation of the relations described

above." We are able to confirm these early observations and in the light of the changes which take place in Ambystoma at transformation, offer an interpretation of the presence of the fourth process connecting the palatoquadrate with the ear capsule. Undoubtedly as in Ambystoma the columella becomes fused with the margin of the fenestra and maintains its connection with the suspensorium through the stilus which is without doubt the cartilaginous process from the fenestral lip to the quadrate cartilage seen by Wiedersheim.

We feel no hesitation in offering this interpretation of the structures in this form even though developmental stages have not been studied by us. The sound-transmitting apparatus in Salamandra is in all essential respects identical with that of Ambystoma in which a very large number of developmentad stages have been studied carefully, permitting an interpretation of the adult condition which without them would be difficult. Fuchs ('07) has figured and described the chondrification of the otic capsule in Salamandra, giving in some detail the formation of the fenestra vestibuli and operculum. Employing the nomenclature of Gaupp, he describes the operculum as formed chiefly by a cutting out of the already chondrified ear capsule and partly by the chondrification of the chondroblastema filling in the fenestra. The latter he recognizes existent from the beginning as an unchondrified portion of the otic capsule. The development of the *Operculum* of Salamandra he undoubtedly gives correctly and in the figures of models of three stages shows it forming upon the medial and caudal sides of the fenestra in the manner stated above just as the operculum is formed in Ambystoma and in Triton presently to be described. He neither discusses nor shows in his figures, however, the process described by Wiedersheim, the detailed development of which in this form would be of particular interest. No hint is given of its origin or relations except in Fig. 3 on page 11 where a slight projection from the dorsal boundary of the fenestra appears to be what we are inclined to interpret as the caudal tip of the columella. A comparison might also be made between his Figs. 3, I, and our Figs. 1 and 23 (Pl. I) of Ambystoma and Fig. 27 (Pl. II) of Triton.

Fuchs gives no intimation of the ages or sizes of the larvæ or

embryos studied. His theoretical conclusions drawn from the development of the operculum in Salamandra will be referred to in the second part of the paper.

Triton and Diemictylus.

In Cope's family of the Pleurodelidæ, the condition of reduction and incorporation,—if we may so state it,—is carried farther than in the form just described,—Salamandra. The connection with the squamosum and palatoquadratum is absent, and the fenestral plate forms the portion of the ear capsule bounding the cephalic part of the fenestra vestibuli above and in front. In the adult, the identity is entirely lost and it would be impossible to recognize the true morphological relations were it not for the condition in the larva. In fact, at the time of our first contribution, the existence of the columella in Diemictylus was not recognized even though larvæ had been examined. At that time we expressed confidence in its presence at some stage in the development of the larva, but thought that it was absorbed or became incorporated,—possibly with the operculum. It was, indeed, subsequently found to be present and incorporated not with the operculum, but with the edge of the fenestra. It was in the light of the conditions in Salamandra that the relations in Diemictylus became clear. The existence of the columella was first determined in a 19 mm. larva, the subsequent examination of Triton larvæ bringing confirmation. In this last form the significance of the morphological relations is more apparent so that it may best be considered first.

Triton cristatus. Through the kindness of Professor Robert Wiedersheim, we were enabled to examine a series of specimens of this form, serial sections being prepared of larvæ 18, 20, 25, 34, 36, and 37 mm. in length. In the smallest individual at our disposal (18 mm.) both operculum and columella are present, of cartilage, the latter fused more or less completely with the crista semicircularis, hence it has been impossible to determine how early this structure appears; whether at any time its proton is as obviously outside the membrana fenestræ as it is in Ambystoma, or whether it undergoes chondrification separate and distinct from the edge of the primary

fenestra, later becoming fused with it. There is some evidence in our series that leads us to believe that it will be found to chondrify as a separate piece of cartilage:—(a) its cartilage differs in its staining from that composing the crista semicircularis, presenting the appearance of "younger" cartilage; (b) it lies outside what might be considered the ideal plane of the fenestra and apparently outside the fenestral membrane; (c) in some of the larvæ a small cleft is left between the crista semicircularis and the columella. This cleft is especially well marked in the 36 mm. larva (Fig. 48, Pl. VII), but present on one side only, being therefore variable in its extent and doubtless simply an indication of imperfect fusion. The columella as in Ambystoma fills in the anterior portion of the primitive fenestra in its dorsal part; if the fusion with the ventral lip occurs early, it is conceivable that the dorsal fusion may be delayed.

As to the mode of formation of the operculum, the evidence is indubitable; it is forming in the "floor" of the ear capsule as a chondrification in the "opercular tissue" (membrana fenestræ) in its caudal and medial portions. In the 18 and 20 mm. specimens, the operculum is already outlined, but broadly continuous on its medial and caudal sides with the cartilage of the floor, and were it modelled, would doubtless present the appearance shown in the model of a 20 mm. Triton tæniatus published by Gaupp ('05, p. 695, Fig. 350). In the older larvæ, save for the larger size of the operculum and its more complete separation from the floor of the otic capsule, conditions have not been essentially changed. A model was made of this region in a 34 mm. larva which is reproduced in Fig. 27 (Plate II). Here the operculum is shown forming in the caudal portion of the fenestra still rather broadly connected with the floor of the otic capsule caudally and medially. The rudimentary fenestral plate is shown fused with the anterior portion of the crista semicircularis. The closure of the anterior portion of the primary fenestra is also being accomplished by a growth of cartilage upon its ventral side. This figure showing the primitive fenestra and its contained cartilages may be directly compared with the stage in Ambystoma shown in Fig. 24, Pl. I, and its diagrammatic elucidation in Text Fig. 1.

Three photographs (Pl. VII, Figs. 48, 49 and 50) of sections from the 36 mm. larval Triton are submitted in illustration of what has been said above. Fig. 48 is through the ear capsule cephalad of the (secondary) fenestra at a point where the columella is fused with the ventral lip of the (primary) fenestra (cf. Fig. 27, Pl. II). It shows the cleft between the dorsal margin and the crista semicircularis whose existence has been mentioned above. It might also be compared with Figs. 28 and 29, Plate XV, of Gaupp's ('93) monograph upon the Chondrocranium of the Frog. Fig. 49 is five sections (75 microns) farther caudad through the columella and just ahead of the tip of the operculum, while Fig. 50 is still farther back (210 microns) behind the caudal end of the columella and through the operculum. The position of the artery and vein may be noted, in comparison with Figs. 8, 9 and 10 of Stöhr ('79). It may be remarked that in the oldest of the larval Tritons examined (37 mm.) the M. opercularis has not yet appeared nor has the operculum become completely separated off from the cartilaginous ear capsule.

By comparing these figures (Pl. VII, Figs. 48-50) and the two similar ones of a Diemictylus larva (Text Figs. 4-5) with the sections through the ear capsule of the larval and transforming Ambystoma (Pl. III, Figs. 31-32-33) the basis of the homologies for Triton becomes evident. In a comparison of Triton and Ambystoma the early appearance of the operculum in Triton is noteworthy. Its proton is already partially outlined at 18 mm. in length, and doubtless recognizable at a still earlier stage, while in Ambystoma its appearance comes only with the beginning of transformation, and in the larva it is a part of the otic capsule. The columella element, on the contrary, while already evident in the youngest Triton larva, becomes more prominent in the later larval stages; in Ambystoma it appears very early. The growth of the columellar plate in Triton during the larval period with an increasing distinctness of demarcation from the crista semicircularis suggests, it must be admitted, the interpretation of a differentiation out of "fenestral tissue" as the fenestra increases in extent. As has been said, the available material does not permit us to determine the early transformations

that take place in the ear capsule in Triton. The presence of a rudimentary columella seems clearly established. The problem of its phylogeny may be better discussed from a comparative view-point.

No trace of a stilus or connection with the squamosum or palatoquadrate was to be found unless, possibly, a scanty group of cells extending from the columella around the outer side of the vena petroso-lateralis was its representative.

In the adult Triton the conditions are much altered. The otic capsule is strongly ossified; the operculum being an oval plate of cartilage filling in the relatively small fenestra vestibuli and projecting back a short distance. On its outer side it gives attachment to a well developed M. opercularis; on its inner side is the cavum perilymphaticum and its backward extension outside the otic capsule is the recessus perilymphaticus. To the otic capsule behind and to the edge of the fenestra the operculum is attached by membrane only. The fenestral margin is osseous behind; dorsal and ventral cartilaginous lips join to form the cephalic border of the fenestra, the cephalic end of the operculum being slightly included. The columella is completely merged with the otic capsule, though doubtless the dorsal and cephalic cartilaginous margin of the fenestra, in part at least, represents it. Figs. 43 (Pl. V) and 44 (Pl. VI) show the relations, shape and cartilaginous consistency of the operculum. The latter figure may be compared with Fig. 42 (Pl. V) of Salamandra in illustration of the more massive character of the operculum in that form. Recurring again to the columella, in these two forms, Triton presents a condition of much greater reduction and incorporation in the absence (in the adult) of a recognizable fenestral plate and stilus columellæ (cf. Figs. 41 and 43, Pl. V).

The development of the otic capsule in Triton has been followed in more or less detail by Reichert '38, Semmer '72, Parker '82b, Wiedersheim '77, and Stöhr '79. From the reduced condition of the columella in this salamander, it was to be expected that its presence, not to mention significance, should be entirely overlooked and that the development of the operculum should be given correctly in all essential points. Hence we find Reichert, Semmer, Wiedersheim, Parker, and finally, Stöhr describing the operculum as formed

out of the otic capsule in this Urodele. Stöhr's classical investigation was undertaken primarily to describe whether or not after all the columella (of reptiles) was not of double origin,—one portion derived from the ear capsule (opercular plate) and a second portion from the hyoid arch, and as a preparatory study it seemed best to him to re-examine conditions in the amphibia (p. 480). Parker, in the meantime, published his first paper, dealing largely with the development of the skull of the Axolotl (to which reference has already been made, p. 562, but including a brief description of the skull of the larval and adult Salamandrina (Seironota) perspicillata. His second paper, dealing with Triton, appeared subsequently to Stöhr's. Wiedersheim ('77) had described (apparently in Triton alpestris) the development of the operculum as cut out of the otic capsule by a circular thinning of the cartilage, which by extension completely separates the operculum from the remainder of the otic capsule as a nearly circular disc.[8] With this mode of development as with Reichert's view that the operculum appeared as a chondrification in the fenestral membrane, Stöhr disagreed. While he examined, apparently, larvæ of different ages, he described, modelled and figured the condition in a 24 mm. specimen. He says: "Vom vorderen Rande des knorpeligen Fensterrahmens entspringt ein kurzer nach hinten gerichteter Fortsatz (O), der auf der häutigen Fenestra ovalis aufliegt. Zu beiden Seiten des Fortsatzes liegen grosse Blutgefässe (die Rinnen sind auf der Figur sichtbar), die bei der Vergrösserung desselben in so fern eine Rolle spielen mögen, als sie durch Druck die knorpeligen Rinnen, welchen sie anliegen, immer mehr vertiefen und schliesslich den Boden der Rinnen zum völligen Schwund bringen. Die Vergrösserung des Fortsatzes erfolgt aber gewiss auch durch eignes Wachstum. Bei Triton cristatus

[8]('77, p. 501). "Kurz nach Verschmelzung der Parachordal-Elemente mit den Gehörblasen sieht man am äusseren Rand ihrer Unterfläche eine ringförmige Zone auftreten, welche bei genauerem Studium sich als eine circuläre Verdünnung der Knorpelwand herausstellt. Letztere schreitet immer weiter fort *und schliesslich hat sich eine rundlich-ovale Knorpelscheibe aus der Labyrinthwand* (Fig. 6, *Fov, Op*) *herausgeschnürt, ein deutlicher Beweis, dass das Operculum der Urodelen ontogenetisch nicht vom Kiemen-Apparat, sondern von der Gehörkapsel selbst herzuleiten ist.*"

sowohl, wie bei Triton tæniatus bleibt der Fortsatz nicht lange mit dem knorpeligen Fensterrahmen in knorpeliger Verbindung; ehe er noch eine Grösse erreicht, schnürt er sich von seinem Mutterboden ab und stellt nun ein freies, auf der Fenestra ovalis aufliegendes Knorpelplättchen dar; das Operculum. * * * *Das Operculum ist demnach ein Theil der knorpeligen Ohrkapsel, hervorgewachsen vom vordern Umfang des ovalen Fensters. Mit dem Hyoidbogen steht es genetisch in keiner Beziehung."* Interestingly enough, the description and figures indicate that the structure he identified as the Operculum was not the Operculum but the Columella. Its shape, connection with the anterior border of the fenestra, and its position between artery and vein, leave small doubt of this. The development of the *operculum* he seems to have entirely missed, and the mode of development advanced by Wiedersheim appears to be more nearly correct, though doubtless chondrification of opercular tissue in the fenestra vestibuli also contributes to its growth. It seems certain that in the growth of the larva both the fenestra and the operculum increase in size, and observation of this enlargement and extension of the rather cleft-like fenestra (*vide* Gaupp '05, Fig. 350) doubtless caused Parker to believe that the oval window arose by "dehiscence," and explains also the mode of origin of the operculum advanced by Semmer and by Wiedersheim. On the other hand, Stöhr's contention that the fenestra exists from the beginning as an unchondrified portion of the ear capsule, is without doubt true for Triton as we find it to be for Diemictylus, but describes the origin of the primary rather than the secondary fenestra. Stöhr, in a year-old Triton, figures the true operculum.

Parker's brief statements ('82b, pp. 198, 199, 203, 206, 209) upon the operculum (Stapes) and fenestra vestibuli (ovalis) in larval and adult Triton (Triton punctatus) are too indefinite to permit of any conclusions being based on them as to what the conditions were. In the adult he comments upon the cartilaginous nature of the operculum (Stapes) and the lack of a stilus (columella).

Diemictylus viridescens. Little need be said of the conditions in this form since in all essentials it resembles Triton closely. In the transformed salamander (red form) as also in the fully adult (Figs.

2-3), the operculum is plate-like, of cartilage, having the same relations to the fenestral margin as in Triton. It is somewhat more massive; the fenestral margin is cartilaginous only in front and above where the cartilage extends back to the caudal end of the fenestra. Below, cartilage extends back only as far as the anterior tip of the operculum. A well developed M. opercularis is present.

During the larval stage the morphological relations are essentially those of Triton larvæ, the vestigial plate being somewhat more closely joined to the crista semicircularis (Fig. 4, *Cr. s.*), but its

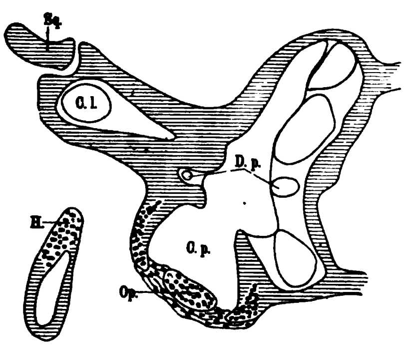


FIG. 2.

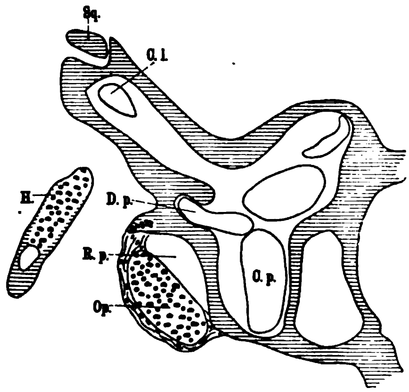


FIG. 3.

FIG. 2. Diemictylus viridescens, land form. *C.l.*, canalis lateralis; *C.p.*, cavum perilymphaticum; *D.p.*, ductus perilymphaticus; *H.*, ceratohyale; *Op.*, operculum; *Sq.*, os squamosum.

FIG. 3. Diemictylus viridescens, land form. *C.l.*, canalis lateralis; *C.p.*, cavum perilymphaticum; *D.p.*, ductus perilymphaticus; *H.*, ceratohyale; *Op.*, operculum; *R.p.*, recessus perilymphaticus; *Sq.*, os squamosum.

ventral edge more evidently outside the membrana fenestræ. At 15 mm. in length, neither columella nor operculum have appeared. In a 17 mm. specimen, the columella is developing upon the fenestral membrane in continuity with the fenestral margin above and in front. The operculum is forming on the medial edge of the fenestra in continuity with the cartilage of the capsule. Aside from growth and a more marked differentiation of the operculum, there has been but slight change in a larva 19 mm. long. At 37 mm. the operculum and also the columellar plate are well developed. The relations

of the two structures may be seen from the accompanying figures, 4-5.

These figures may be compared with the similar figures of the 36 mm. Triton larva (Pl. VII, Figs. 49 and 50). Fig. 4 may also be compared with Fig. 41, Plate V, of Salamandra and Fig. 32, Plate III, of transforming Ambystoma.

Adequate descriptions of the "sound-transmitting apparatus" in Diemictylus are lacking. Parker ('82a) describes the condition in both larva and adult (pp. 179, 181), but each statement is brief and without significance; more significant is his comment when

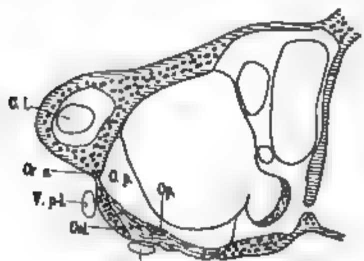


Fig. 4.

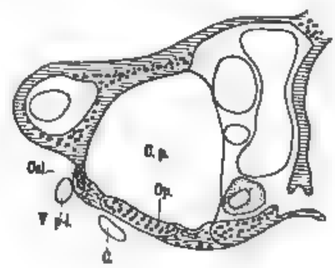


Fig. 5.

Fig. 4. Diemictylus viridescens, larva 37 mm. long. *C.*, arteria carotis interna; *C.l.*, canalis lateralis; *Col.*, columella; *C p.*, cavum perilymphaticum; *Cr.s.*, crista semicircularis; *Op.*, operculum; *V.p-l.*, vena petroso-lateralis.

Fig. 5. Diemictylus viridescens, larva 37 mm. long. *C.*, arteria carotis interna; *Col.*, columella; *C.p.*, cavum perilymphaticum; *Op.*, operculum; *V.p-l.*, vena petroso-lateralis.

characterizing the skull of Spelerpes (See foot note on p. 578). Cope ('88) is not sufficiently detailed and Wiedersheim ('77) does not particularly emphasize the relations in this portion of the skull of Diemictylus.

Plethodontidae.

Representatives of all the genera of this family have been examined as follows: Batracoseps, Hemidactylium, Manculus, and Autodax, the adult stage only; Gyrinophilus, Plethodon, and Stereochilus, both larva and adult; Spelerpes, adult and a series of twelve developmental stages of larvæ from 15 to 55 mm. in length.

In the fenestra vestibuli of the adult there is a single plate, irregularly oval in outline and free from the ear capsule except on its ventro-cephalic margin where a fusion is found (Pl. X, Fig. 67). From the cephalic and dorsal portion of this plate there projects upwards and forwards a slender stilus (Fig. 67) which in the adult articulates with both quadrate and squamosum. It is slender in all forms except Batracoseps where it is absent or vestigial. In the caudal portion, the fenestral plate extends behind the caudal margin of the fenestra and swells outward, forming a prominence in this region. The cavity of this prominence is an outward and backward extension of the cavum perilymphaticum. In a relatively deep depression on the caudo-lateral aspect of this prominence the M. opercularis is attached. The fenestral plate in the Plethodontidæ is, as are all the related parts, finer and much less massive than in the families already considered. The stilus is relatively a long and slender rod between the vena petroso-lateralis above and the arteria carotis interna and facial nerve below. The lips of the fenestra vestibuli remain cartilaginous and are connected with the fenestral plate by membrane only, save in the cephalo-ventral portion mentioned above.

The inner and outer bony plates so characteristic of the columella in other forms are here co-ossified, the cartilage persisting only at the circumference. In the central portion of the plate the cartilage which is subsequently replaced by bone, varies markedly in thickness even in the same genus,—for example, in Spelerpes bislineatus it is small in amount and early replaced by bone, while in Sperlerpes ruber quite the reverse is true. A similar comparison could be made between genera. The ossification of the fenestral structures in this family corresponds to the ossification of the skull as a whole, both in time and extent.

Accompanying this marked ossification of the plate there is complete ossification of the base of the stilus; distally it is composed of a shell of bone enclosing a cartilaginous core. In regard to the relation of the peripheral end of the stilus, it should be stated that the articulation with the squamosum, quadrate and palatoquadrate mentioned above applies only to the adult. In the larvæ of the forms

studied (Gyrinophilus, Plethodon, Stereochilus, Spelerpes) the connection was with the squamosum only. In the adult there is a very wide variation, from a close articulation with the squamosum only (as in Manculus) to an intimate connection of the stilus with a cartilaginous process of the palatoquadrate, as in Stereochilus, Autodax and Plethodon. The other genera show an intermediate condition; in Hemidactylium and Spelerpes the connection with the squamosum is the closest, while in Gyrinophilus there is an equally close articulation with the subsquamosal process of the quadrate; in no one of them was the cartilaginous process of the palatoquadrate as well developed as in Stereochilus, Autodax, and especially Plethodon.

The variation in the connections of the distal end of the stilus is undoubtedly associated with the inclination of the suspensorium to the long axis of the skull. During the period of growth, due to the relative displacement of parts, the distal end of the suspensorium is "drawn" forward, bringing its long axis more nearly parallel with that of the skull.

The definitive fenestra vestibuli of the Plethodontidæ is large and lateral in position, more nearly representing the primary fenestra of other urodeles,—a condition recognized by Parker.[9] The columella is correspondingly large, nicely filling the opening, and projecting slightly back of it, as presently to be described. The plan of ossification in the columella is so characteristic that we have come to consider it as the Plethodontid type.

The M. opercularis, though absent in the larva, is a well developed structure in the adult. It attaches to the caudal portion of the fenestral plate, which there possesses a decided excavation occupied by the tendon of the muscle, giving the "scooped out" appearance noted by Parker.

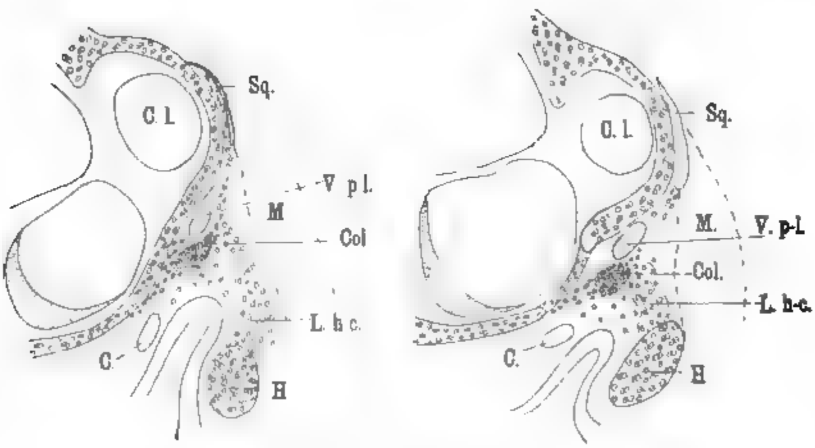
[9]Parker, '82, p. 199. "The under face of this ear capsule (in Spelerpes) is very different from that of most high "Urodelous" skulls.

"In those massive *typical* Caducibranch skulls just described, *e. g. Notophthalmus* (Pl. XVII) and *Cynops* (Pl. XVIII), the vestibule is in the form of a smooth *bulla*, with the stapes set on behind; and that plate is either quite soft or very slightly ossified; it is also relatively small.

"In *Spelerpes* (Pl. XXI, Figs. 2, 3, and Pl. XVIII, Fig. 10) the vestibule is but little protuberant; its fenestra is lateral, and corresponding with the stapes, very large."

Despite the depression for the M. opercularis the ear capsule has in this region a bulging appearance due to the growth of the fenestral plate backwards beyond the margin of the fenestra vestibuli. Fig. 47 (Pl. VI) shows not only that the prominence has extended beyond the margin of the fenestra, but also that within the prominence there is a recessus which is continuous with the cavum perilymphaticum.

Earlier in this paper it has been shown that in Ambystoma and others there is a perilymphatic prominence in the region of the



FIGS. 6 and 7. Plethodon cinereus, embryo. *C.*, arteria carotis interna; *C.l.*, canalis lateralis; *Col.*, columella; *H.*, ceratohyale; *L.h-c.*, ligamentum hyo-columellare; *M.*, musculus cephalo-dorso-mandibularis. *Sq.*, os squamosum; *V.p-l.*, vena petroso-lateralis.

fenestra vestibuli formed by the outward and backward growth of the operculum and that to the lateral aspect of this structure the M. opercularis is attached. Within the perilymphatic prominence is the recessus perilymphaticus, a caudal continuation of the perilymphatic cavity. In these respects there is a striking similarity between the caudal portion of the fenestral plate in the Plethodontidæ and the operculum of other forms. Further than the similarities mentioned in the preceding paragraph there is, in the adult, no evidence as to the constitution of the fenestral plate in the Plethodontidæ. In the light of development, however, the condition is

somewhat better understood. Eleven larvæ of Spelerpes bislineatus ranging in length from 15 to 55 mm. were studied by means of serial sections. Just when the columella makes its appearance we can not say, but in larvæ 15 and 17 mm. long there is present a delicate cord of cells outside the ear capsule extending from the under side of the squamosum towards the fenestral membrane to which it is not closely related at this stage. In a larval Plethodon cinereus (Figs. 6 and 7) of a similar stage of development this cord is composed of a greater number of cells and is consequently more com-

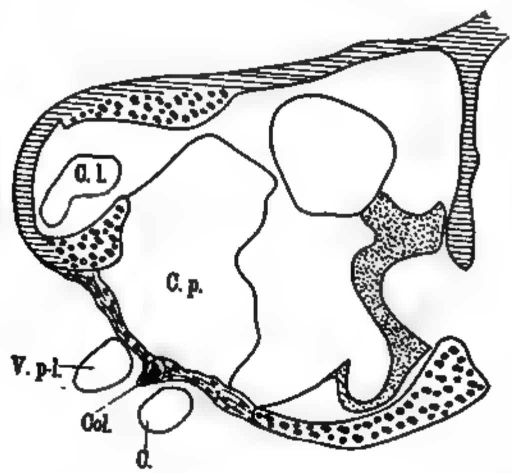


FIG. 8. Spelerpes bislineatus, larva 23 mm. long. *C.*, arteria carotis interna; *C.l.*, canalis lateralis; *Col.*, columella; *C.p.*, cavum perilymphaticum; *V.p-l.*, vena petroso-lateralis.

pact and larger. Here also, as in Spelerpes, this group of cells is not closely connected with the fenestral membrane. It extends forward to the under side of the squamosum and apparently is joined to the ceratohyal by a less marked cord of cells. Figs. 8 and 9 from two sections 25 microns apart may serve to illustrate the extraotic position of the columella. Comparison with the figures of like stages of Ambystoma and Cryptobranchus is suggested.

In Sperlerpes larvæ 23 mm. long the lower end of this cord of cells has become intimately associated with the fenestral membrane at the cephalo-ventral margin of the fenestra. At this point the fenes-

tral plate remains permanently fused with the ear capsule. Chondrification has occurred, forming a stilus and a small fenestral plate (Figs. 8 and 10).

From the place of its attachment the fenestral plate gradually extends backwards, growth being the result of the deposition of cartilage in the free margins of the plate, particularly the caudal. Thus successive rings are added until the plate fills the opening in the ear capsule. In the caudal portion of the fenestra vestibuli the mem-

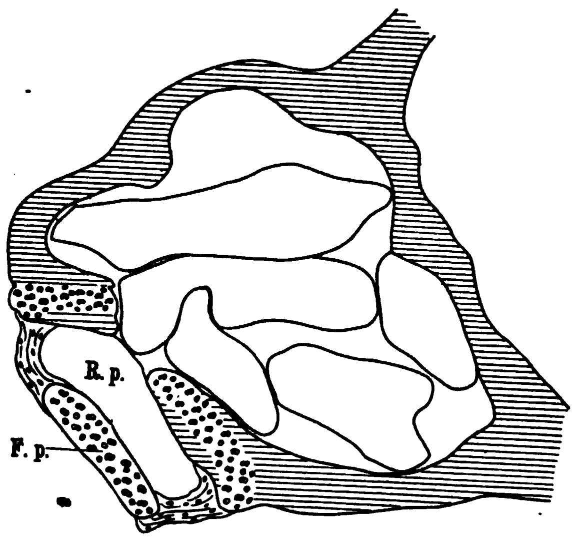


FIG. 9. Spelerpes ruber, larva 71 mm. long. *F.p.*, fenestral plate; *R.p.*, recessus perilymphaticus.

brane forms an outpocketing or prominence (Fig. 12) long before it is invaded by cartilage, but before transformation the extension of the prominence behind the lips of the fenestra is slight if present at all. The prominence forms the outer walls of a recessus which has the same relations as that of the adult. Until transformation there is no indication of the M. opercularis, it apparently having no function until adult life is assumed. The conditions in the adult Plethodontidæ are well illustrated by the photographs of Gyrinophilus in Figs. 45, 46, 47 (Pl. VI).

It appears that the definitive plate of the adult is the result of a direct and continuous growth of cartilage in the membrane which covers the foramen vestibuli. At no time during development are there found separate centers of chondrification in either stilus or fenestral plate.

There appears to be a wide divergence between the sound-transmitting apparatus in the Plethodontidæ and that in Ambystoma. This seems particularly true of the development, and as a consequence is also true of the homology of parts. A brief review of the development of the fenestral elements in the forms thus far considered may, therefore, render the situation easier to grasp. In Ambystoma the ear capsule chondrifies early and the columella fills the fenestra vestibuli. At transformation (there being no room for growth) the operculum is cut out from the cartilage of the ear capsule itself; an adaptation, it might seem, to mechanical needs. In Triton and Diemictylus the columella relatively early fuses completely with the

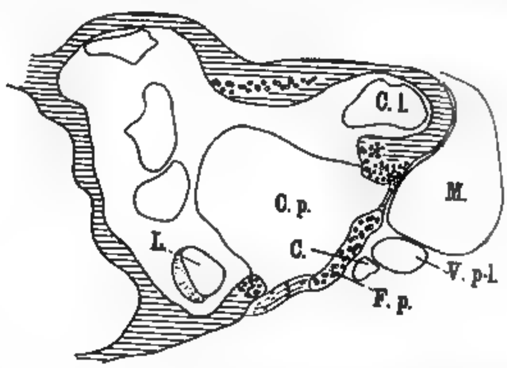


FIG. 10. Spelerpes bilineatus, larva 43 mm. long. *C.*, arteria carotis interna; *C.l.*, canalis lateralis; *C.p.*, cavum perilymphaticum; *F.p.*, fenestral plate; *L.*, lagena; *M.*, musculus cephalo-dorso-mandibularis.

ear capsule, leaving the foramen free. Here it is found that, while there is a slight cutting out of the operculum from the ear capsule, it results largely from a growth of the cartilage cephalad into the fenestral membrane. The situation in the Plethodontidæ differs from either of these. The columella, when first coming into intimate relation with the ear-capsule, is small as compared with the size of the for-

amen which increases in size with the growth of the skull. The early ossification of the ear capsule renders impossible the formation of an operculum by either the cutting out process or by forward growth into the fenestral membrane. A comparison of Figs. 11 and 12 will help to make clear that the membrane filling the caudal portion of the fenestra corresponds in its position and relation to other parts to that portion of the fenestra in Ambystoma which is occupied by the operculum. This, together with the formation of a prominence by the fenestral membrane in this region, which when chondrified affords attachment for the M. opercularis, suggests that it is opercular tissue. Taking this view it is perhaps not inappropriate to consider that the caudal portion of the fenestral plate in the Plethodontidæ represents the operculum of other forms.

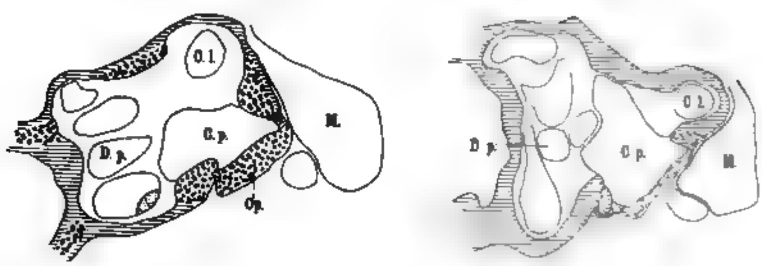


Fig. 11. Ambystoma punctatum, transforming larva. *C.l.*, canalis lateralis; *C.p.*, cavum perilymphaticum; *D.p.*, ductus perilymphaticus. *M.* musculus cephalo-dorso-mandibularis; *Op.*, operculum.

Fig. 12. Spelerpes bislineatus, larva, 55 mm. long. Lettering as in Fig. 11.

This is from the viewpoint of groups in which the operculum is formed as a separate structure. Looking at it from the reverse point of view the Plethodontidæ might be considered as representing the less specialized condition. It is conceivable that in those forms in which an operculum is developed the columellar blastema became fused with the edge of the primitive fenestra both in front and behind, so that when it came to chondrification there were almost of necessity, developed two plates: (1) the fenestral plate of the columella joined to the otic capsule in front, and (2) the operculum joined to the ear capsule on the caudal and medial side. The operculum would thus be a dissociated part of the fenestral plate. In

the Plethodontidæ, due possibly to an early fusion of the columellar blastema in front only, such a division of the plate does not occur. It seems quite possible that a comparative study of the primitive fenestra in urodeles might afford some evidence of this view. What bearing this interpretation might have upon the periotic origin of the operculum is evident.

Desmognathidae.

Desmognathus fusca. In this species, the only member of the small family examined, the "sound-transmitting" apparatus mark-

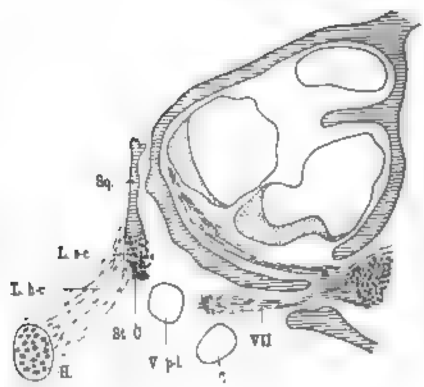


FIG. 13. Desmognathus fusca, larva 26 mm. long. *C.*, arteria carotis interna; *H.*, ceratohyale; *L.h-c.*, ligamentum hyo-columellare; *L.s-c.*, ligamentum squamoso-columellare; *Sp.*, os squamosum; *St.C.*, stilus columellæ; *V.p-l.*, vena petroso-lateralis; *VII.*, nervus facialis.

edly resembles in its general structure and relations that of the Plethodontidæ just described. In fact, they are of the same type. A bony plate with cartilaginous border fits into the fenestra and projects caudad upon the outer wall of the recessus perilymphaticus. The caudal portion is concave externally, and in the depression there is inserted the M. opercularis. The cephalo-ventral border is continuous with the cartilaginous border of the fenestra. The stilus is osseous with a cartilaginous core, the distal portion being of cartilage alone. Two figures of an adult, one (Fig. 15) through the caudal portion showing the concave fenestral plate and the recessus; the second (Fig. 14) through the insertion of the stilus, may be

directly compared with the sections through the same regions in the plethodontid, Gyrinophilus (Pl. VI, Figs. 46 and 47). Similar comparison may be made with Spelerpes (Figs. 6 and 7).

The relations of the stilus to the squamosum, quadrate, facial nerve, artery and vein, have been described in some detail by Kingsbury ('03, pp. 321-325) for larva and adult, two sizes of each, and as our investigations have not added significant details, it will be sufficient to state in confirmation of the description there given that while in the larva the stilus is most closely joined to the ventral edge of the squamosum (Fig. 13); in the adult it becomes shifted so as to articulate closely with the os quadratum, less closely with the cartilaginous process of the palatoquadrate. The relation to artery, vein and nerve is that typical of the majority of urodeles.

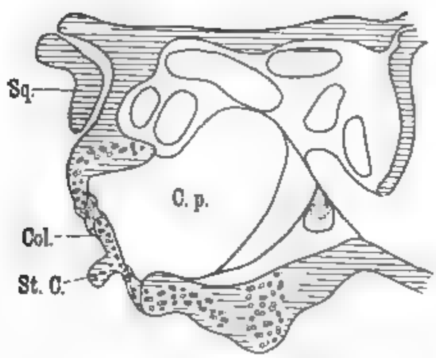


Fig. 14. Desmognathus fusca, adult. *Col.*, columella; *C.p.*, cavum perilymphaticum; *Sq.*, os squamosum; *St.C.*, stilus columellæ.

An examination of young larvæ and embryos which would determine the origin or origins of the stilus and fenestral plate, has not been undertaken. The mode of insertion of the stilus upon the fenestral plate, as shown in Fig. 14 (compare also Pl. VI, Fig. 46, Gyrinophilus), might suggest that the stilus alone developed outside the otic capsule, as the description of Parker would indicate. Since the columella in Desmognathus doubtless develops in essentially the same manner as in the Plethodontidæ (Spelerpes, Plethodon) reference may be made to the description of its development in that family, as given on p. 580.

Desmognathus possesses a short but well developed ligamentum hyo-columellare, in this respect also agreeing with many of the Plethodentidæ. In Fig. 13 it is indicated in the larva.

TYPHLOMOLGE.

A single adult 95 mm. long was studied by means of serial sections and a model of the entire skull in the otic region. The fenestra vestibuli is filled by a single plate as in the Plethodontidæ, connected by a long and slender stilus with the suspensorium. On the cephaloventral margin the fenestral plate is fused with the ear capsule.

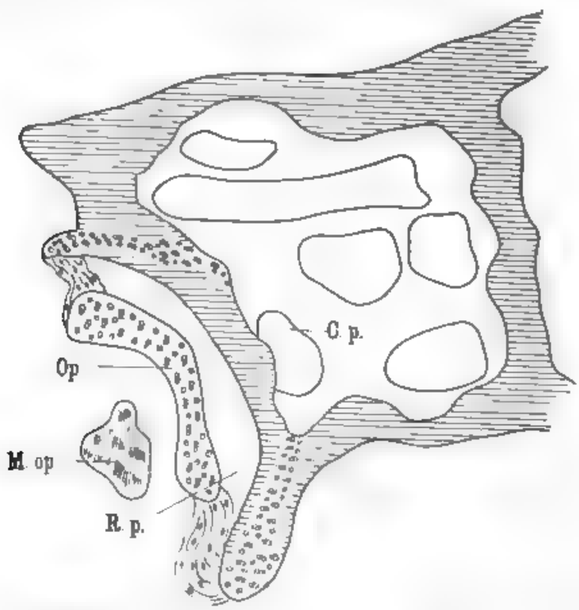


FIG. 15. Desmognathus fusca, adult. *C.p.*, cavum perilymphaticum; *M.op.*, musculus opercularis; *Op.*, operculum; *R.p.*, Recessus perilymphaticus.

The stilus is relatively longer than in any of the other forms examined. This is probably due to the extreme flattening of the skull, which has brought the long axis of the suspensorium more nearly parallel with that of the skull, thus throwing the attachment of the stilus to the suspensorium farther cephalad. It seems likely that this flat condition of the head is the result of an adaptation to sub-

terranean life where a wedge-shaped form is more convenient for making progress in narrow quarters.

Miss Ellen Tucker Emerson, 2d ('05), states in substance that the operculum is not connected with the suspensorium, and her figures show a short stilus, labelled columella, projecting freely from a basal portion in the fenestra vestibuli called operculum. Serial sections and the model of the specimen studied by us show that the columella is morphologically connected with the suspensorium but interrupted. On the right side of our specimen the stilus begins to grow smaller in diameter a litle beyond the middle of its extent and finally disappears for a distance of 210 microns. Then it appears again, gradually assuming its normal diameter, and continues uninterruptedly to the suspensorium. Here it is joined to the squamosum, the os quadratum and the palato-quadrate (Pl. II, Fig. 28). Between the free ends of the segments is a well defined ligament within which a few cartilage cells are found at intervals.

On the left side there are three segments (Pl. X, Fig. 68) produced by two interruptions. One of these corresponds in position and extent with the single interruption on the right side. The second occurs just before the stilus joins the suspensorium and is about the same in extent as the first. On this side the distal or third segment extends for a distance along the ventral edge of the squamosal, joining the edge of the os quadratum as well, but without relation to the palato-quadrate. It should be noted in this connection that Kingsbury ('03) described the stilus in adult Spelerpes as connected with a rod of cartilage lying along the ventral edge of the squamosum, a condition similar to what is found on the left side of our specimen of Typhlomolge.

It may be questioned whether the interrupted condition of the stilus in Typhlomolge results from tension and a consequent separation of what otherwise would remain, as developed, a continuous bar of cartilage, or is reminiscent of the condition found in the frog where there are separate centers of chondrification. It should be recalled, however, that in the urodeles where development has been studied, chondrification of the stilus and columella is continuous. Furthermore it is to be noted that in the Plethodontidæ there is a

loose connection of the stilus with the suspensorium, probably due to the tilting of the latter in its relation to the long axis of the skull. In Typhlomolge this tilting of the suspensorium is extreme and it is, therefore, a fair question as to whether or not the segmentation in the stilus is the result of tension during development. The attachment of the stilus to both suspensorium and columella are at the same horizontal level, there being a slight outward and downward curvature as shown in Plate III, Fig. 28.

The relation of the stilus to the blood vessels and nerves in this region is that found in Necturus, namely, the vena petroso-lateralis and the ramus jugularis of the facial nerve are above, while the main trunk of the facial nerve and the internal carotid artery are below. This condition is illustrated by Fig. 28 (Pl. III) and Text-figure 16.

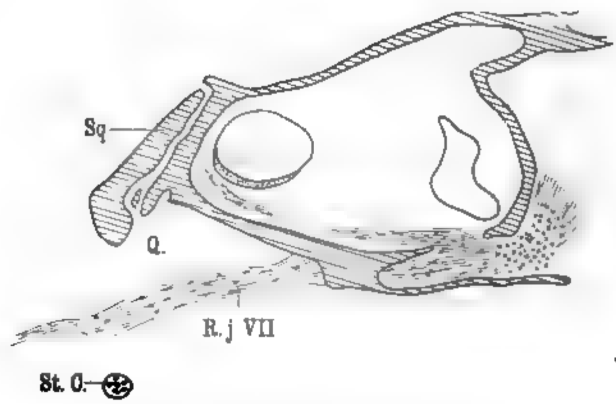


FIG. 16. Typhlomolge, adult. *Q.*, os quadratum; *R.j.VII.*, Ramus jugularis VII.; *St. C.*, stilus columella; *Sq.*, os squamosum.

The fenestra vestibuli is irregularly elliptic in outline as is the fenestral plate. The dorsal and ventral portions are not filled by the plate, there being a relatively wide space both above and below filled only by membrane. In the caudal portion there is a slight outward swelling forming a prominence which projects slightly beyond the caudal lip of the fenestra and which contains a small but well defined recessus within. The M. opercularis is absent.

The lips, both of the fenestra vestibuli and the fenestral plate,

remain cartilaginous throughout the greater part of their extent, the bony portion of the plate being much thinner than the margin as in the Plethodontidæ. At its base the stilus is composed entirely of bone (Fig. 17) which gradually becomes a sheath surrounding a core of cartilage. In the distal half (Fig. 16) the stilus is composed of cartilage alone.

Between the distal end of the ceratohyal and the otic region of the skull is a wide sheet of fascia, the caudal portion of which is attached to the stilus and in this region becomes a relatively strong ligament between the columella and hyoid (Pl. X, Fig. 68).

Developmental stages have not been studied, but it appears that in Typhlomolge the type of sound-transmitting apparatus is essentially that of the Plethodontidæ.

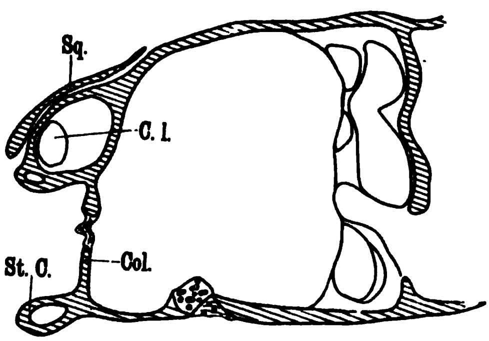


Fig. 17. Typhlomolge, adult. *C.l.*, **canalis lateralis;** *Col.*, **columella;** *St.C.*, **stilus columellæ;** *Sq.*, **os squamosum.**

Necturus.

Although the relations and development of the otic region of the skull in Necturus have been already quite well worked out by several persons, because of its historic interest in this connection and the general acceptance of its low systematic rank, it has been included for brief consideration. In illustration of the conditions in this form four photographs are introduced, Figs. 57, 58, 59 (Pl. VIII), and 60 (Pl. IX).

Miss Platt ('97), p. 430, described the early development in the ear capsule in Necturus. In a 19 mm. larva the "operculum" is

pre-cartilage, forming neither from the otic capsule nor the fenestral membrane, but independently lying primarily anterior to the fenestra. She suggested at this time the possible homology of the urodele operculum with the pars interna plectri which is supported in this paper; but evidently without much faith in its correctness, for in a footnote in which she states her objection to the term "operculum" she adds that this cartilage (operculum, *i. e.*, columella) is not the equivalent of the "columella" (plectrum) of the Anura and is of questionable homology with the "stapes" of higher vertebrates.

Kingsbury ('03) examined the early development in Necturus. He confirmed Miss Platt's results and in addition described the primary connection with the squamosum and the cells underlying it: "At this stage, the operculum is just beginning to chondrify as a distinct center, and from it a chord of cells is continued forward, ventral to the vena jugularis and the ramus jugularis, to the cells surrounding the developing squamosum, becoming continuous with them a short distance (50 microns) back of the processus oticus quadrati. The cells are of course continuous with those of the squamosum and also with the cells between that bone and the quadratum, so that the squamosum, the quadratum, and the ligament-anlage, may be said to be joined together by a common mass of cells. In the just hatched larva, likewise, the ligament-anlage clearly goes to the underside of the squamosum and inserts itself between that bone and the processus oticus quadrati, so that it might be interpreted as going to both structures. As soon as the connective tissue fibers develop, however, the relation is seen to be with the squamosum and not with the quadratum. In later stages a strong ligamentum squamoso-columellare develops, which connects the stilus columellæ to the columellar process of the squamosum."

Wilder ('03) in a monograph upon the Skeletal System of Necturus takes, however, a different view. He regards the operculum (columella, our term) as a "detached portion of the otic capsule" basing his view upon the condition in a 44 mm. larva which was essentially the same as in a 26 mm. individual examined by him. In the light of the work by Stöhr on Triton and Siredon he regards the statements of Miss Platt as unfounded, admitting, however,

that the proton described by her might represent "a true columella or hyomandibular cartilage which may become fused with the true operculum," although he could find no trace of such a double origin. In comment on the above it may be said that to determine the first development it is necessary to go back of the condition in a 26 mm. larva as was done by Miss Platt. There is certainly no indication of a double origin, although the increase in size in the columella of Necturus, as in Ambystoma (p. 556), admits of two possibilities of interpretation. The development of the operculum as described by Stöhr in Triton and Siredon has been discussed on p. 573.

The ramus jugularis VII passes over the ligament (Pl. VIII, Fig. 58), as in Proteus and Typhlomolge described above.

The relations of the columella, squamosum and facial nerve in Necturus are well known through the work of Cope, Drüner, Kingsbury and Wilder, though the significance of the relations has not been adequately considered.

Huxley's classic paper on the skull of Necturus was in respect to his description of the relation of the columella, facial nerve, and suspensorium incorrect and misleading, occasioning a wrong idea of the urodele type, persistent even up to the present time. We find no trace of his ligamentum suspensorio-stapiale, over which the facial nerve passes. Operculum (our use) and M. opercularis are lacking.

Proteus agrees in all essentials with Necturus (Wiedersheim, Drüner, Kingsbury).

Cryptobranchidae.

Cryptobranchus alleghenensis. Through the generosity of Mr. B. G. Smith, of Syracuse University, who kindly sent us a series of embryo, larval and adult specimens, we were enabled to examine the relations in this interesting form with quite satisfactory results.

As the publications of Wiedersheim ('77), Parker ('82b) and Cope ('88) have shown, the Columella in the adult possesses a well developed stilus which articulates with the under (inner) surface of the squamosum. This relation is strikingly shown in the series of sections through the head of an adult 140 mm. long (Pl. VII,

Figs. 54-55; Pl. VIII, Fig. 56) which was at our disposal. The squamosum, furthermore, is the only skeletal element to which the columella is attached, save the os pterygoideum which works its way well up on the inner surface (Pl. VII, Fig. 54) of the palatoquadrate and whose upper edge is somewhat loosely connected with the end of the stilus columellæ. As though determined by the excessive flattening of the head in this form, the mandibular end of the palatoquadrate is well back and lateral, while the cranial attachment by means of the usual three processes is unusually far forward (cephalad). The whole suspensorium is therefore rotated from an "ideal" transverse position, and it would seem as though this displacement might well explain in a mechanical way (a) why the stilus columellæ joins the under surface of the squamosum instead of its caudal edge as in so many of the forms; (b) how it is possible for the os pterygoideum to come into such close relation to the columella; (c) the absence (in the *young* adult at least) of a connection of the stilus with the palatoquadrate or os quadratum.[10]

A second interesting feature found in this skull is the presence of what might be interpreted as a Ligamentum hyo-columellare (Pl. VII, Fig. 55, L. h. c.) which is essentially a thickening of the fascia covering the inner (under) surface of the M. cephalo-dorso-mandibularis. It extends from the ceratohyal to the outer surface of the stilus, extending with it to its attachment to the squamosum. As this ligamentous thickening of the fascia is relatively more marked in the larva, it will be mentioned again in connection with that stage.

The columella appears to ossify in the typical way; at the stage of our specimen it consists of a cartilaginous body (Pl. VII, Fig. 55; Pl. VIII, Fig. 56) with an inner and outer plate of perichondral bone, the latter extending out upon the stilus for a distance. The distal portion possesses no bony sheath and it was doubtless this that led Parker to distinguish here two elements, a *Stapes* (bony and

[10]From this bone as a center the ossification of the quadrate cartilage apparently proceeds. Kingsbury referred to it as "bone X," Gaupp has suggested tentatively the homology with the os quadrato-maxillare of Anura. Its final interpretation requires additional comparative investigation.

fitting into the fenestra) and articulated with a *Pharyngohyal,*[11] consisting of cartilage. This is, of course, incorrect, due to the inadequacy of the method of gross dissection, upon which he based his conclusions.

From the caudal edge of the palatoquadrate a rather delicate process of cartilage extends back to the ceratohyal to which it is applied, curving slightly over its upper surface. The name of Epihyal which Parker gave to this process of the quadrate is likewise certainly incorrect. Cope ('88) has termed this the "Hyo-suspensorial cartilage;" it might more correctly be called *Processus hyoideus palatoquadrati,* since an *articulation* with the quadrate as described by him is not found. In other respects the description of Cope is essentially correct. Wiedersheim, likewise, describes the squamosal connection of the stilus and the position of the facial nerve correctly, though he apparently overlooked the condition here in the general portion of his paper.

Larval Cryptobranchus. Serial sections were made through the head of four Cryptobranchus larvæ whose lengths were, respectively, 28 mm., 34 mm., 45 mm., and one just hatched. Since in these series the morphological relations are in all essentials the same, it will be sufficient for the purposes of this paper to describe briefly the relations in the one which is of intermediate size (34 mm.), and supplement this with comments on some interesting features in the youngest,—the newly hatched larva.

The columella in this larva (34 mm.) consists of a roughly oval plate of cartilage resting upon the membrane closing the fenestra vestibuli. From the cartilaginous border of the fenestra the columella is separated by the membrane everywhere except at the cephalic edge where it articulates with the cartilaginous ear capsule at the crista semicircularis. In larvæ 28 mm. and 45 mm. long, the fenestral plate does not come into articular relation with the carti-

[11] Parker in his earlier paper ('76, pp. 559 and 587) referred to this cartilage as homologous with the elasmobranchian "Spiracular cartilage" and the annulus tympanicus of the Frog, the facial nerve passing below it. In the second paper, however, in which he terms it a pharyngohyal, the facial nerve is described as passing over it.

lage of the car capsule, so that doubtless this is a variable feature. In the adult there appears to be a very slender cartilaginous connection. The portion of the fenestra vestibuli not occupied by the columella is thus a crescent of somewhat horse-shoe shape.

The stilus of the columella arises gradually from the cephalic half of the fenestral plate, passing at first more laterally and then in a curve cephalad and slightly dorsad to become closely attached to the lower edge of the squamosum. In its course it passes between the vein and artery, as is typical, the vein being above (Pl. VII, Fig. 51). The facial nerve is entirely ventral to it, though the jugular branch and ramus communicans IX come very close, the latter lying at first upon the dorsal side of the columella; it slips over the outer side, however, and joins the R. jugularis in gliding under the stilus just as the latter joins the squamosum.

The sheet of fascia covering the inner surface of the M. cephalo-dorso-mandibularis possesses two thickenings of morphological importance. The more dorsal of these (Ligamentum hyo-columellare) arises over the outer side of the ceratohyal, curves around its upper surface and passes forward to join the stilus columellæ at its bend and, as a sheath upon its outer side, accompanies the latter to its articulation with the squamosum. Fig. 51 (Pl. VII) illustrates the location of this ligament in its course from hyoid to columella and shows the muscle "bellying against" the ligament as a full sail against a rope. A portion of this seems to have been Parker's stapedio-suspensorial ligament. The more ventral and band-like ligamentous thickening passes from the ceratohyal to the caudal edge of the quadrate. It curves around this element and a portion of it joins the tendon of the M. cephalo-dorso-mandibularis at its insertion on the os angulare. This ligament must embody the ligamentum hyo-suspensoriale and as well the ligamentum hyo-mandibulare. In connection with the former, in the adult is developed the cartilaginous process of the palatoquadrate already described. Whether this process develops from an independent center or not, and at what stage it appears, cannot be determined from the material at hand.

In the larva, the suspensorium has not the "rotated" position that

it has in the adult, and the columella has no connection with the palatoquadrate, os pterygoideum or os quadratum. Furthermore, it is to be noted that it articulates with the lower edge of the squamosum and not with its under surface.

The newly hatched Cryptobranchus is of interest in this connection for two reasons: (a) the columella is represented by a condensation of cells from which a cord of cells passes cephalad (Pl. VII, Figs. 52-53) and dorsad to the group of cells in whose midst the squamosum is just appearing as a homogeneous scale of bone; (b) the columella at this stage is pre-cartilage and is distinctly forming outside the ear capsule. The chondrocranium is cartilaginous, the fenestra clearly demarcated, and the precartilaginous columella external to the membrana fenestræ (Fig. 52). The development at this stage closely parallels that of Necturus, as already described (p. 590). It seems to us safe, therefore, to add Cryptobranchus to Necturus and Ambystoma as a form showing the extra-otic appearance of the columella, and its early connection with the squamosum. It is likewise noteworthy that the columella in all the larvæ examined shows no cartilaginous connection with the otic capsule; and in the adult the fusion is very slender,—if indeed it exists. The source of the cells that form the columella could not be determined from the material at hand, although two embryos were examined. Neither operculum nor opercular muscle are developed.

It is interesting to note in concluding that Cryptobranchus is the only form in which there has been general agreement as to the connection of stilus with squamosum; not so, however, the relation to the facial nerve. Both Wiedersheim ('77) and Parker ('82b) described the relation correctly and subsequently altered their statements.

Megalobatrachus. From the description of Parker ('82b), Wiedersheim ('77), Osawa ('99), as from the dissection of a single specimen in connection with this study, suffice it to state that it shows essentially the same relations as Cryptobranchus. Osawa (as quoted) describes the stilus as joining the palatoquadrate. Parker states that the hyo-suspensorial cartilage (his epihyal) *articulates* with the palatoquadrate; in Cryptobranchus there is continuity.

Amphiuma.

In Amphiuma a single plate fills the fenestra vestibuli and is free except on its cephalic end where it is fused with the ear capsule which is cartilaginous. The very large stilus is articulated at its distal end with the squasmosum and continuous with a process of the palatoquadrate. Its relation to the facial nerve and blood vessels is typical. On both inner and outer surfaces of the fenestral plate there is a layer of bone (Fig. 18) which is continued for a short

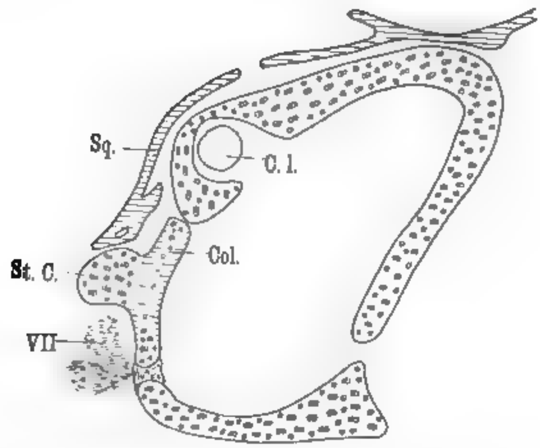


Fig. 18. Amphiuma means, adult. *C.l.*, canalis lateralis; *Col.*, columella; *Sq.*, os squamosum; *St.C.*, stilus columellæ; *VII.*, nervus facialis.

distance upon the base of the stilus. A distinct but not strong ligamentum hyo-columellare is present. Its diagrammatic representation is given in Pl. X, Fig. 71.

The fenestral plate becomes narrower in its caudal third and finally tapers to a point. In that portion of the ear capsule forming the caudal margin of the fenestra there is a pronounced prominence within which there is a continuation of the perilymphatic cavity of the ear (Fig. 20).

While complete developmental stages have not been studied, sections through the head of a larva soon after hatching, a transforming individual and an adult furnish some data regarding development. In the youngest larva the fenestral plate is relatively small

and free from the ear capsule all round. Although closely associated with, it appears to be wholly outside of, the fenestral membrane.

At transformation the columella is fused in front with the ear capsule and just fills the opening. Below and behind the columella a portion of the floor of the ear capsule becomes greatly thickened, especially in its lateral half, which is almost completely separated from the capsule (Fig. 19). In this stage there are a few muscle

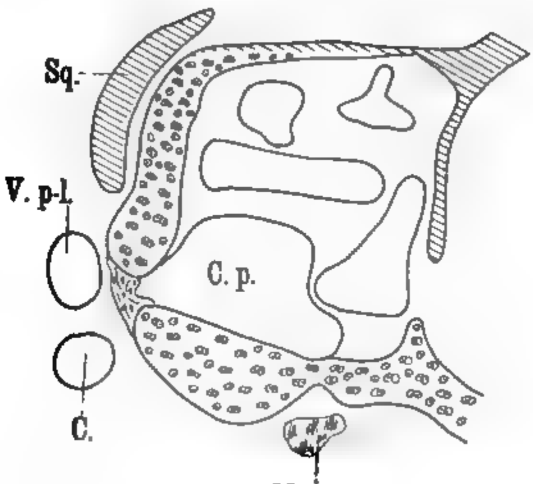


Fig. 19. Amphiuma means, transforming larva. *C.*, arteria carotis interna; *C.p.*, cavum perilymphaticum; *Sq.*, os squamosum; *V p-l.*, vena petroso-lateralis; *M.i.c.i.*, a portion of the musculus intertransversarius capitis inferior.

fibers partly differentiated off from the M. intertransversarius capitis inferior which have a slight attachment to this portion of the ear capsule.

This portion of the floor of the ear capsule which was thickened and partly separated off in the transforming individual is in the adult very much thickened, forming the pronounced prominence which encloses an extension of the perilymphatic cavity as shown in Fig. 20. The M. intertransversarius capitis inferior comes into close relation with the prominence of the adult, but there is no differentiation of a distinct opercular muscle.

By comparing Fig. 11 and Fig. 31 (Pl. III) of Ambystoma and Fig. 50 (Pl. VII) of Triton it is evident that this portion of the otic floor corresponds in position to the operculum. It would seem as though at transformation a beginning of operculum formation was made which does not go through to completion.

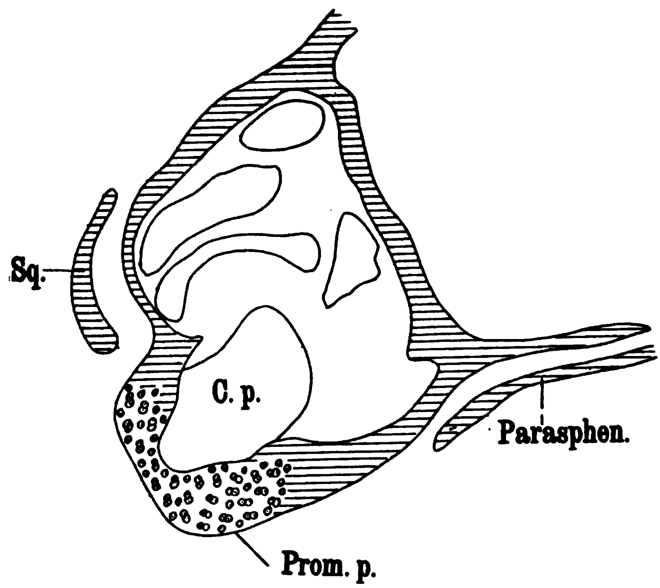


FIG. 20. Amphiuma means, adult. *C.p.*, cavum perilymphaticum; *Parasphen.*, os parasphenoideum; *Prom. p.*, prominentia perilymphatica. *Sq.*, os squamosum.

SIREN.

The only material examined was an adult specimen 133 mm. long. The fenestra vestibuli is here, as in some other forms, filled by a single plate which is cartilaginous in our specimen although Cope ('88) states that it is bony in this species. It is elliptic in outline, facing outwards and downwards with a short stilus standing almost vertical to the plate and slight inclination being in a backward and downward direction. The connection of the columella with the suspensorium, if it ever existed, has disappeared. The relation of the stilus to the blood vessels and nerves in this region is typical.

The fenestral plate is fused throughout its entire cephalic margin with the ear capsule. This fusion is much greater in extent, relatively, than in either Typhlomolge or the Plethodontidæ.

The ceratohyal is much produced caudally, its falcate distal portion extending beyond the otic region. A short distance before the caudal extremity is reached there arises from the dorsal edge a broad and strong ligament extending forwards for insertion upon the fenestral plate (Pl. X, Fig. 72). The stilus projects directly into this just cephalad of which there arises another, the hyo-suspensorial ligament, which passes cephalad for insertion upon the palatoquadrate. These ligaments are considered by Cope as one, namely, a hyo-suspensorial ligament extending from the *quadrate* across the ear capsule to the exoccipital. Parker treats them as two separate and distinct ligaments. That portion extending to the quadrate he calls the hyo-suspensorial while to the columellar portion he applies the name suspensorio-stapedial. Functionally they are probably to be considered as distinct, but in serial sections they appear to be thickenings of the same sheet of fascia.

The short and free stilus projecting into the ligamentum hyo-columellare is more comprehensible in the light of the segmented condition of this structure in Typhlomolge. Thus in Siren all suspensorial communication of the fenestral plate with the exterior, such as is found in other forms, is cut off. But it will be noted that the ligamentum hyo-columellare in this form is strongly developed which together with its firm attachment to the fenestral plate may compensate for the absence of the usual skeletal connections. The relation of the stilus to the facial nerve and blood vessels is that found in the majority of forms.

Three figures (Pl. IX) illustrate the relations of the columella, stilus and hyo-columellar ligament. In Fig. 61 the short stilus is shown projecting out into the dense ligament, the diminutive plate joined to the margin of the fenestra by connective tissue. Fig. 62 is through the caudal end of the columella of the opposite side. In Fig. 63 the section is through the perilymphatic prominence, a caudo-lateral extension of the ear capsule. Slightly farther forwards the cartilage is hollowed out by a small recessus. The fenestra

and the caudal lip of the columella appear in the lateral wall of the prominence. In all essentials, save as noted, the sound-transmitting apparatus of the adult is like that of Amphiuma.

General.

In perusing the preceding portion of this paper, it will have become obvious that considerable confusion in the interpretation of the sound-transmitting apparatus in Amphibia,—particularly the Urodela,—has been caused by discrepant statements and conflicting descriptions of the conditions existing in the different forms. The differences that apparently existed concern principally (a) the relation to the suspensorium, (b) the relation of the facial nerve to the stilus columellæ, (c) the mode of development of the fenestral structures.

The Suspensorial Connection. Gaupp in his paper on the sound-transmitting apparatus of Vertebrates ('98) was led to the conclusion that there existed two types of connection between the suspensorium and the skeletal element filling the fenestra vestibuli,—one above and one below the facial nerve, and the same view has been taken by Drüner ('03). Gaupp later ('05) says: "Die oft citierte Angabe von Wiedersheim, dass der Nerv bei allen Urodelen ohne Ausnahme über diese Brücke hinweglaufe, ist irrig; vielmehr scheint der Verlauf der Nerven *ventral* von der fraglichen Brücke das häufigere zu sein. Letzteres findet sich bei Amphiuma (Hay 1890, auf Grund eines von Prof. Norris hergestellten Modelles kann ich diese Angabe bestätigen), Siredon (Hasse 1873, Parker 1877) und zahlreichen anderen Urodelen (Proteus, Desmognathus fusca, Spelerpes bilineatus, nach soeben veröffentlichten Untersuchungen von Kingsbury); der Verlauf des R. jugularis facialis *über* die erwähnte Verbindung findet sich bei Necturus (Huxley) und Proteus (Drüner, Kingsbury). Es sind somit 2 verschiedene suspensorio-columellare Brücken aus einander zu halten, eine über und eine unter dem Facialis (Gaupp 1899)."

For this divergence of statement, Huxley seems to have been primarily responsible, inasmuch as in Necturus he described a "Ligamentum suspensorio-stapediale" and stated that "the hyo-

mandibular branch of the seventh nerve (VII) passes above this ligament to its distribution, just as it passes above the *Columella auris* in the frog."

The real connection of the stilus with the special process of the squamosum[12] (*Processus columellaris*) he seems to have missed entirely. The reference to Huxley of a recognition of such a connection by Gaupp in the passage quoted above is incorrect. It should be remembered, however, that Huxley's observations were based upon minute dissections, in which a strand of fascia could easily be made to assume the appearance of a ligamentous structure, and the obvious passage of the hyomandibular division of the seventh nerve *over* the columella in the frog and the relation in mammals would incline one *a priori* to a similar interpretation in urodeles. Wiedersheim appears to have accepted his statement of relations, and without paying special attention to the point, gave as the universal condition in urodeles that the facial nerve passed above the suspensorial connection. Huxley's description doubtless influenced his friend, W. K. Parker,[13] who in several forms described the facial nerve as below the columella, yet sometimes located it above, or was vague in his descriptions.

One result of this study is to show that a "suspensorial connection" does indeed exist, in all save four of the salamanders examined (Diemictylus, Triton, Siren, Batracoseps) the nervus facialis being below and in front (see, however, p. 610). The connection is not primarily with the palatoquadrate, as has been heretofore believed, but with the bone, partly overlying the palatoquadrate and partly over the lateral semicircular canal of the ear, which we have regarded as *squamosum*. This primary connection of the columella through

[12]The correct relation was described subsequently by Cope ('88, '89), Wilder ('03), Drüner ('11), and Kingsbury ('03); the relation to the facial nerve, by the last two.

[13]Parker, '77 (p. 559), in a footnote says: "Professor Huxley pointed out this anomaly to me, showing me that this ligament cannot correspond to the "suspensorio-stapedial" ligament of *Menobranchus* (*op. cit.*, p. 192)." The reference is to the squamoso-columellar ligament in *Ambystoma*, which is, of course, *above* the facial nerve. See footnote on page 562 for Parker's description.

its stilus with the squamosum is now reported[14] for Necturus maculatus, Proteus, Typhlomolge, Typhlotriton, Spelerpes bislineatus and ruber, Gyrinophilus prophyriticus, Hemidactylium scutatum, Plethodon cinereus, Stereochilus marginatus, Autodax lugubris, Manculus quadridigitatus, Desmognathus fusca, Ambystoma punctatum, Chondrotus tenebrosus, Cryptobranchus allegheniensis, Megalobatrachus maximus.

In certain of the forms, however, at transformation,—before or after it,—the connection of the stilus tends to shift to the palatoquadrate, presumably in the change of the position and direction of the suspensorium to which Wiedersheim called attention ('77). In this displacement of parts as we interpret it, the squamosum, as in Ambystoma, comes to lie more on the dorsal surface of the palatoquadrate. In certain forms a special process of the palatoquadrate develops (e. g., Plethodon, Amphiuma) which may reach a relatively great length (Amphiuma). Hence we see how the more obvious connection has become accepted as the typical one, and the primary connection with the squamosum[15] is overlooked, even though occurring throughout life as the direct articulation in many of the forms. If the anatomical relation of parts is such that the palatoquadrate does not come into the proximity of the distal end of the stilus in the shifting, a connection with it is not established,—as in the case of Cryptobranchus (young adult) where the connection of the stilus moves from the caudal edge to the under side of the squamosum. Whether the stilus columellæ maintains the primary relation with the squamosum or becomes more closely joined to the palatoquadrate, any physiological value it may possess as a "suspensorial connection" remains unaffected, so closely is the lower

[14]Cope, '89, describes the correct condition in Necturus and Proteus (p. 22); of the remaining urodeles he says: "The stapes [columella] has no connection with the suspensorium in the adult except in the Cryptobranchidæ and Amphiumidae. It is connected with the suspensory cartilage, which is continuous with the quadrate cartilage in the latter families, and in the young of other Urodela" (p. 29).

[15]The development of the stilus columellæ has not been studied in Salamandra, nor in Amphiuma has the earliest development been yet worked out (see Kingsbury, '03, p. 325). The squamosal connection will doubtless be found in all salamanders possessing a well developed stilus.

end of the squamosum joined to the quadrate. From a morphological viewpoint, however, it is not a matter of indifferent significance. The connection of the columella with the squamosum and its formative cells is a primary one, while the direct articulation or junction with the palatoquadrate is only secondarily established. The significance of the relation becomes more impressive when the development of the columella is considered. In the forms in which the early development has been traced,—Necturus, Ambystoma, Cryptobranchus, Spelerpes, Plethodon,—before cartilage has appeared in the columella, when the squamosum is but a delicate scale of bone, a cord of cells proceeds from the proton of the columella to the cells underlying the forming bone. The developmental relations will be considered again in connection with the question of hyomandibular homology.

Columella and Operculum. A second complication exists in Amphibia due to the existence of two structures that are found fitting into the fenestra vestibuli, and the failure to recognize this fact has added another source of confusion in the elucidation of the relations in this group. It is the first of these two elements, distinguished by us as *Columella,* which possesses a suspensorial connection. The second, termed by us the *Operculum,* possesses no such relation. In its typical form as it exists in the adult Ambystoma, Diemictylus or Salamandra, the operculum is a spheroid filling in the definitive fenestra with whose lips it is connected by membrane only or possesses a slight cartilaginous connection at its caudal end. It may be massive (spheroidal) as in Salamandra, or more plate-like as in Triton. The cephalic end is included by the lip of the fenestra; the caudal end projects freely, covers the recessus perilymphaticus externally and affords attachment to the M. opercularis. In the families of the Plethodontidæ and Desmognathidæ the condition is characteristic and unique; the oval window has fitted into it a plate whose cephalic portion possesses a well developed stilus and whose caudal portion offers attachment to the M. opercularis and covers externally a recessus perilymphaticus; it seems therefore to *represent* both columella and operculum.

The statement of Gaupp ('05) in reviewing the Amphibian sound-transmitting apparatus (p. 605), that only by a stretch of the

imagination could an extra-otic origin be ascribed to the element filling the fenestra vestibuli in this group, was made in the light of the condition existing in Triton and the fragmentary developmental evidence already at hand, and without knowledge of the existence of two structures in urodeles. It applies, therefore, with full force to the development of the operculum. The columella, however, develops in quite a different manner, and here the evidence of an extra-otic origin is much stronger. Killian ('90) first described this structure as developing outside the ear capsule in Ambystoma, and Miss Platt ('97) in Necturus advanced the same view. Kingsbury subsequently examined the condition in larval and embryo Necturi and came to the same conclusion. In this paper we have shown evidence of an entirely similar mode of origin of the columella, outside the fenestral membrane, in Cryptobranchus, Spelerpes, and Plethedon, and confirmed Killian's observations on Ambystoma. Supplementary evidence of an extra-otic origin for the columella is to be found in the fact that from the first, before chondrification has begun, the columella is connected by a dense grouping of cells with the squamosal cells around the outer side of the vena petroso-lateralis.

With the growth of the fenestral plate of the columella it becomes associated or fused with the cephalic edge of the fenestra. This is not, however, a primary connection but a secondary one. Hence the statement that has been made (Winslow, Stöhr) that the columella grows out of the cephalic edge of the window is not correct. In the descriptive portion of this paper, the difficulty in determining just what occurs in the chondrification of the plate of the columella has been pointed out. Even though the columella grew through the incorporation of otic tissue, its origin from without the otic capsule would not be invalidated, which is supported by its relation before chondrification and its early and intimate connection with the subsquamosal cells.

The tendency of the columella to become fused with the cephalic cartilaginous margin of the fenestra is in some forms carried to an extreme, and results in a more or less complete incorporation of the structure into the ear capsule by extensive fusion with it. In the Ambystomidæ its boundary is still distinguishable by the charac-

teristic inner and outer bony plates, and by the stilus. Salamandra lacks the ossification, the incorporation appears more intimate but the stilus is persistent. In Triton and Diemictylus stilus and ossification are both lacking and incorporation into the edge of the fenestra is complete.

Attending the fusion of the columella, there is the formation of the operculum to inherit its position and function as a fenestral structure. Concerning its origin and development there is not, as in the case of the columella, opportunity for uncertainty. In Ambystoma, in which it appears late,—at the end of transformation,—it is cut out of the floor of the otic capsule medial to the fenestra. In Diemictylus and Triton, in which it appears early, "cutting out" must play a more secondary part, and marginal growth by chondrification of opercular tissue seems more important. It occupies in either event the same position and seems to be a detached portion of the otic capsule, although extensive cartilage formation in it may give it a thickness several times that of the otic capsule. It undergoes no ossification, remaining cartilaginous throughout life.[16] Its characteristic features, negative and positive, are the lack of connection with the skeleton outside the ear capsule, and the attachment of the M. opercularis.

The fusion of the columella causing a more or less extensive filling in of the cephalic portion of the fenestra vestibuli necessitates the recognition of primary, secondary and definitive fenestræ, of somewhat different boundary and location, as in the Anura (Gaupp, '93). The question of in how far the cephalo-caudal succession of fenestral elements or the (essentially) cephalo-caudal extension of the fenestra itself is an expression of the play of factors of relative growth of parts,—otic capsule, suspensorium, etc.,—is simply raised. It is hardly necessary to state that the primary character of the fenestra as an unchondrified portion of the otic capsule, as affirmed

[16]It is interesting to find Parker ('82a) commenting on this condition; on page 199 he says: "One more point of interest is to be noted here: the lowest Perennibranchs have their stapes thoroughly ossified (*i. e.*, the columella); the highest Caducibranchs, like the Batrachia, have it (*i. e.*, the operculum) soft; here in *Spelerpes* it ossifies early, and becomes a very perfect and elegant shutter to that small oval window."

by Stöhr and more recently by Fuchs ('07) as contrasted with an appearance secondarily, by dehiscence or absorption, is abundantly established. It must be understood, however, that this applies only to the primary fenestra, while in the formation of the secondary and definitive fenestræ, in some forms, at least, the extension is accomplished essentially as a "dehiscence." The developmental transformations undergone by the primary fenestra require a more detailed study in a number of salamanders before a full interpretation can be made.

In the Plethodontidæ and Desmognathidæ, where the single fenestral plate possesses some of the characters of operculum and columella combined, the development has been followed in *Spelerpes bislineatus*. There is no evidence of a fusion of two structures, the cartilaginous and bony plate which bears the stilus by growth gains the territory which in Ambystoma is occupied by the operculum and may therefore be regarded as representing that structure without embodying it.[17]

On plate X are set forth in schematic form the morphological relations of the two structures under consideration as they occur in typical forms. Examining the conditions in the Urodela, we find that they may, with the figures of this plate as illustrations, be divided into seven groups, the characters being compared in tabular form on page 607.

Under these seven groups the forms studied distribute themselves as follows: Group I; Necturus, Proteus (Typhlomolge). Group II; Larval Ambystoma and urodele larvæ in general, Cryptobranchus, Megalobatrachus, Amphiuma. Group III; Adult Ambystoma, Adult Chondrotus, probably other members of the Ambystomidæ. Group IV; Salamandra, and possibly some of the Ambystomidæ. Group V; Diemictylus, Triton, undoubtedly Salamandrina and other Pleurodelidæ. Group VI; Siren. Group VII; the Plethodontidæ (as examined),—Typhlotriton, Spelerpes, Gyrinophilus, Hemidactylium,

[17]The differences between the Ambystomidæ and the Plethodontidæ in respect to the presence and absence of an operculum, are paralleled in the Anura by the similar differences in the Frog (as an example of the type) and Pipa. Gaupp's very interesting discussion of the interpretation in the last case ('98, p. 1065) presents the problem for the first case as well.

Plethodon, Stereochilus, Autodax, Manculus (Batracoseps). The Desmognathidæ (Desmognathus fusca.)

Two forms are exceptional; *Batracoseps,* which otherwise falls under group VII, possesses a vestigial stilus and therefore lacks the connection with the suspensorium, usually well developed in the Plethodontidæ. The interesting form *Typhlomolge* is plethodontid in the character of the fenestral plate, but possesses a fragmented stilus. The interesting course of the R. jug. VII over the stilus, and the absence of the M. opercularis, however, places it in Group I.

TABLE TO SHOW THE SEVEN TYPES OF "COLUMELLA AURIS" IN URODELES.

Group	Fig.	Columella					Operculum	M. operc.
		Fenestral plate	Fusion with fenestral margin	Stilus	Connection of stilus with	Relation of R. jug. VII to St.		
I.	68 69	present	none or slight	present	squamosum	above	absent	absent
II.	70 71	present	none or slight	present	squamosum or Sq. and Pal-.Quad.	below	absent	absent
III.	64	present	extensive	present	squamosum and palato-quadrate	below	present	present
IV.	65	present, cartilage	complete	present	palato-quadrate	below	present	present
V.	66	present	complete	absent	absent		present	present
VI.	72	present	moderate	present?	ceratohyal		absent	absent
VII.	67	prseent	slight	present	squamosum, quadrate, or palato-quadrate or all	below	not separately developed	present

Briefly classified from the point of view of the existence of two fenestral structures, *Columella* and *Operculum,* these forms may be divided into the following groups: A, groups I and II; the columella present, free, connected with the suspensorium, no operculum or opercular muscle. B, groups III and IV; the columella present, fused with the otic capsule, connected with the suspensorium, operculum and opercular muscle present. C, group V; columella vestigial, fused with the ear capsule, no connection with the suspensor-

ium. Operculum and opercular muscle present. D, group VII; columella present, joined to otic capsule, connected with the suspensorium; the opercular muscle present, the operculum not developed as such. Up through the groups I to V, evidence of indubitable value is presented of the incorporation and loss of an element (columella) with an attendant loss of its primary connection, a substitute making its appearance (the operculum). The m. opercularis, absent in groups I, II and VI, present in the others, appears to deserve the name given it by Gaupp ('93), since in the Urodela it possesses characteristic attachments and is not a portion of another muscle (Levator anguli scapulæ). When an operculum is developed, an opercular muscle is present, while its insertion in group VII is suggestive, as is also equally, its absence in groups I and II. From the examination of larvæ, it should be stated, however, that it appears to be absent in all urodeles in the larval state. It will be referred to subsequently in connection with the problem of the function of the urodelan "sound-transmitting" apparatus.

Comparison with Anura. In the first contribution a comparison was made of the conditions found in Ambystoma to the "columella auris" of the frog, and further investigation has strengthened us in the acceptance of the homologies then advanced,—the columella with the plectrum (pars interna plectri), the operculum being homologized in the two groups. The resemblances and differences between the two forms may perhaps best be presented in tabular form, in parallel columns the resemblance being presented first, enumeration of differences following. The relations in the frog are taken from Gaupp ('93, '05).

The first of the differences (No. 7) is of no marked significance, since in other Anura (e. g., Dactylethra, Parker, Gaupp '98) the plectrum may overlap the operculum. The next two contrasts partake more of the nature of resemblances than of differences, hence items 10 and 11 are the only points of difference needing comment here, a detailed discussion not being intended, since they are doubtless the ones that will be regarded as the most weighty.

As to the tenth item, it is only necessary to recall the numerous instances of precocious and postponed development of homologous

	Frog.	Ambystoma.
1.	Two independent elements (*a*) Pars interna plectri (*b*) Operculum.	Two independent elements (*a*) Columella (*b*) Operculum.
2.	The plectrum develops in the cephalic, the operculum in the caudal portion of the secondary fenestra.	The columella develops in the cephalic, the operculum in the caudal portion of the secondary fenestra.
3.	The operculum chondrifies in the opercular tissue and becomes joined to the cartilaginous margin of the fenestra on its dorso-caudal side; becomes completely separated.	The operculum is cut out of the ear capsule, remaining connected longest at its caudal end; becomes completely separated.
4.	The plectrum chondrifies as an independent center out into the dense tissue connecting it to the palatoquadrate.	The columella chondrifies as an independent center in dense tissue connecting it with the squamosum (and palatoquadrate).
5.	The plectrum becomes connected with the ventral (cephalo-ventral) edge of the fenestra.	The columella becomes fused with the cephalic (cephalo-ventral) edge of the fenestra.
6.	The M. opercularis inserts upon the Operculum.	The M. opercularis inserts upon the Operculum.
7.	The cephalic end of the operculum *overlaps* the fenestral plate (pseudoperculum) of the plectrum.	The cephalic end of the operculum *underlies* the columella.
8.	The cephalic portion of the secondary fenestra closes, *excluding* the pseudoperculum.	The cephalic portion of the secondary fenestra closes, *including* (incorporating) the columella (fenestral plate).
9.	A cephalic extension of the cavum perilymphaticum is beneath the pseudoperculum (Ductus fenestræ).	A caudal extension of the cavum perilymphaticum is beneath the operculum (Recessus perilymphaticus).
10.	The operculum develops first; the plectrum at transformation.	The columella develops first; the operculum at transformation.
11.	The hyomandibular nerve passes *above* the plectrum.	The hyomandibular nerve (VIIth) is *below* the stilus columellæ.

structures in different forms (Heterochronia) to appreciate that the relative reversal of sequence in frog and salamander is not intrinsically important. Among the Urodela themselves we have an instance of partial reversal, the operculum appearing early in Triton (about 18 mm.) and late in Ambystoma (at transformation).

The opposite relation of the nervus facialis to the plectrum and stilus columellæ, is perhaps a more serious difference, since it is just this criterion of relative position of sound-transmitting apparatus and nerve that has been considered of decisive moment in the determination of homology. As has been stated above, Huxley introduced confusion into the interpretation in Amphibia by faulty recognition of indifferent connective tissue as the equivalent of the frog's plectrum, hence the course of the facial nerve came to be interpreted as *over* the suspensorial-columellar ligament or stilus, whereas in all forms examined just the opposite relation holds,—the facial nerve is *below* (cephalad or ventrad of) the columella, with three exceptions,—Necturus, Proteus, and Typhlomolge,—and in these cases the *jugular branch alone passes above while the rami mandibulares, internus and externus, are below* and in front of the columella.

If the different relation of the facial nerve to the columella in Urodela and Anura is prohibitive of the plectrum-columella homology, there is necessary the recognition of three morphologically distinct squamoso-columellar connections in tailed amphibia, (1) in the Proteida, (2) in Typhlomolge, (3) the remaining urodeles. This, it is felt, is contrary to the ontogenetic evidence. There is involved in this point the broader question of the value of the relation of nerve to skeletal structure as a criterion of homology. The real value of such a test of homology has already been questioned by one of us (Kingsbury, '03, p. 333) and a few instances given of variation in the relation of nerve, ligament and muscle,—instances which could, of course, be easily multipled many fold; for example, in the relation of the hyomandibular bone or cartilage to the hyomandibular nerve, in fishes, etc. It was not deemed desirable to introduce here further consideration of such evidence, as it would involve work along broader comparative lines than was desirable at this time. Adherence is given to the view entertained in the first contribution,—

that the columella and its suspensorial connection is homologous throughout the urodele group, and no valid reason is known why the homology should not be extended to include the Anura as well. Inasmuch as a study of the relations and development in that group has not been made, the homology of columella and plectrum is not presented with the emphasis of personal investigation.

Ligaments. The only muscle that is in the region of the head involved in this study is the *Musculus cephalo-dorso-mandibularis* (*M. depressor mandibuli*). It has its origin largely, and in some of the forms entirely, from the squamosum, and inserts by means of a longer or shorter tendon upon the retro-articular process of the os articulare. Beneath the muscle, between it and the ear capsule, palatoquadrate, hyoid and mandible, is the space filled in with connective tissue containing the nerves and blood-vessels. The tissue next the muscle is denser and comes into intimate relation with the squamosum, palatoquadrate, stilus columellæ, ceratohyal, and mandible. (For illustration, see Figs. 43, 51, 55, 61.)

This submuscular fascia appears to be the foundation, out of which, by thickening of different portions three ligamentous structures may be formed:—(a) Ligamentum hyo-suspensoriale (palato-quadrate), (b) Ligamentum hyo-mandibulare, (c) Ligamentum hyo-columellare. These may all be present in the same species, weakly or strongly developed. Of these the last two have long been recognized (Huxley '74) and are in general well described; the hyo-columellar ligament, however, has not been as adequately considered and is of more interest here because of its connection with the columella. It is best developed in Siren (Fig. 61, 62, 63, Pl. IX), but its presence has been mentioned in the first part of this paper in Amphiuma, Cryptobranchus, Gyrinophilus, Spelerpes, Desmognathus; and seems to be more or less well developed in the Plethodontidæ generally. It will be referred to subsequently in connection with the discussion of the function of the urodelan apparatus. It was not recognized in Ambystoma, Triton, Diemictylus or Salamandra.

A ligamentum palatoquadrato-columellare corresponding to Huxley's suspensorio-stapedial ligament described by him in Necturus it noticeably absent in that form as well as in other urodeles.

Beneath the facial nerve, between columella or operculum and palatoquadrate, is only loose connective tissue, denser in some forms it is true,—especially Siren which possesses well developed hyo-columellar and hyo-suspensorial ligaments giving a less direct suspensorio-columellar bridge of dense connective tissue. It does not seem in any form to possess relations of functional or morphological importance as a "suspensorial" connection of the "sound-transmitting" apparatus.

While the presence or absence and relative development of these ligaments appears to be an expression of the mechanical needs, requirements of support in the nature of a physiological adaptation and therefore secondary phylogenetic importance, their existence may possibly have a deeper significance; the ligamentum hyo-columellare, for example, indicating a primary relationship of columella to the hyoid arch.

The junction of the ceratohyal with the palatoquadrate is quite constant. It is in relation to the hyo-quadrate ligament that the processus hyoideus palatoquadrati is developed in so many forms (see Wiedersheim '77, p. 533).

The diagram reproduced as Fig. 21 illustrates the relations of these three ligaments.

The Hyomandibular-Symplectic Homology. It may be safely stated that from the phylogenetic side the hyomandibular homology of the Amphibian sound-transmitting apparatus is at present generally accepted, as may be seen from the statements in the works of Wiedersheim and Gaupp which were cited (p. 552) as expressing the more recent interpretation. In the earlier form of the theory, however, only a portion was given a hyoid or hyomandibular homology; Reichert, Huxley, Parker, and others regarding the operculum as purely of otic origin.

This hyomandibular homology has been reiterated despite a dearth of evidence from the ontogenetic side. In the Anura, it is true, the embryological evidence has been furnished especially by the monograph of Gaupp, and it has seemed to support the partial homology of the older workers,—if supporting it at all. No direct connection has been found with the ceratohyal in development. In

the Urodela the condition is less satisfactory. Parker, Wiedersheim and Stöhr had emphatically declared the origin of the operculum from the ear capsule and the absence of any association in development with the hyoid arch.

More recently in a paper before the Anatomische Gesellschaft Fuchs ('07) rejected completely the hyomandibular homology[18] of the amphibian structures, basing his conclusions upon the otic origin of the operculum in Salamandra (See p. 568). The presence of a stilus was regarded by him as secondary, the operculum without stilus representing the primitive condition. In the discussion, the homology with the hyomandibulare was upheld by several. Gaupp at that time ('07, pp. 31 and 32) stated his conception of the primitive "Columella auris" as consisting of an operculum and a stilus, the latter articulated with the palatoquadrate. Since the hyomandibulare in fishes is, in many forms, between the palatoquadrate and the otic capsule, the connection of the stilus with the palatoquadrate strongly suggests the homology. He admitted the lack of ontogenetic evidence, but pointed out the difficulty attending the delimitation of what might be hyal blastema from the periotic blastema. Since the upper end of the hyoid arch closely adjoined the otic capsule, blastema of the hyoid arch, it is easily conceivable, might be early incorporated with the periotic, and the operculum might develop apparently as part of the ear capsule and nevertheless be of hyoid origin. In his rejoinder Fuchs (pp. 33, 34) affirmed his belief that the operculum without stilus was the more primitive; that the fenestra arose as a result of the action of a "biological factor" within the ear itself upon the assumption of terrestrial life; that the "rubbing" of the hyomandibulare could in no wise have caused the appearance of the fenestra vestibuli, since in the numerous fish forms

[18]Fuchs ('07, p. 24): "Ich erachte das Operculum bezw. Operculum + Stilus der Urodelen für homolog dem Otostapes der Reptilien und beide für homolog dem Stapes der Säugetiere. Alle drei halte ich ontogenetisch für Abkömmlinge der Gehörkapsel. Auch in phylogenetischer Hinsicht leite ich auf dieselbe zurück und bin ferner der Ansicht, dass sie nicht mit der Hyomandibula der Fische zu vergleichen sind." "Für das Operculum, eventuell Operculum + Stilus, der Urodelen wird dem ja wohl niemand mehr widersprechen. . . ."

in which it does come in contact with the periotic cartilage, no trace of a thinning or fenestration results. Commenting on the position of the hyomandibulare between palatoquadrate and the otic capsule, he expressed the conviction that we must look for the ancestors of terrestrial vertebrates in the low elasmobranchs (Notidanidæ and Pro-Selachia) in which the hyomandibulare has no part in the suspension of the jaw, but affords the hyoid arch an independent articulation with the skull.

Since our results bear directly on the problem and from some points of view, at least, seem to strengthen the homology of the amphibian columella auris with the hyomandibulare, illuminating some of the obscure points of development and relation, it seems desirable to consider it briefly from the following view-points: (a) the extra-otic origin of the columella, (b) the relation to the palatoquadrate, (c) the connection with the squamosum, (d) the relation to the facial nerve, (e) the relation of the columella auris to the ceratohyal.

As Fürbringer pointed out in the discussion of the paper of Fuchs, Salamandra is highly specialized and not a form upon which to base conclusions of general applicability. This has been markedly illustrated in this very problem. For the present, the operculum (our use) may be regarded as a part of the otic capsule both in this and the other forms that possess this structure. Fuchs, however, dealt with but half the problem, as has been shown (p. 568). By other workers, in other forms evidence has been given of an extra-otic origin of a part, at least, of the fenestral structures:—In Necturus by Miss Platt and by Kingsbury (not published); in Ambystoma by Killian and by ourselves in this paper; in Cryptobranchus, Spelerpes and Plethodon, in this paper. In these salamanders, and doubtless in all forms possessing a well developed columella (our use), the first appearance of the sound transmitting apparatus is as a group of cells outside the otic capsule. Of this the evidence seems quite strong; it is only necessary to refer once more to the figures illustrating the condition (Pl. IV, Fig. 39; Pl. VII, Figs. 52 and 53; Text Figs. 6 and 7). In the growth of this blastema in close association with the otic capsule, the chondrification as stilus and fenestral plate, there is introduced the difficulty mentioned by Gaupp,

namely, that of distinguishing cells of extra-otic origin from the periotic blastema. It has, in fact, been so far impossible in Ambystoma and Spelerpes to determine whether or not the fenestral plate of the columella embodied a periotic element. It may be said, however, that in its chondrification and growth the stilus is an integral part of the columella as a whole and not an element from outside secondarily fused with the plate,—representing, therefore, a structure which could by itself be homologized with the hyomandibulare, as was done by Parker.

The articulation of the stilus columellæ with the palatoquadrate, which had been mentioned, as quoted above, by Gaupp (cf. Wiedersheim '06, Gaupp '05) as the significant relation for the hyomandibular homology, has been shown to be a connection secondarily established during growth and development apparently due to a shifting of the connection from the squamosum to the palatoquadrate, in many forms a longer or shorter process of that cartilage developing with which it is articulated or fused. If this connection is in the nature of a secondary adaptation,—and this interpretation is the more probable,—its phylogenetic significance becomes doubtful. There is, however, an association of the two structures of a primary ontogenetic character and suggestive of profound significance. It is to be recalled that in those forms in which the early development of the columella has been traced, the cell mass constituting the proton of the columella is directly connected with the cells between squamosum, the otic process of the palatoquadrate and the otic capsule external to the lateral semicircular canal. If a connection with the palatoquadrate is to be considered of value in determining the hyomandibular homology, it would seem to us, therefore, to be expected that in the displacement of the hyomandibulare from the suspensorium, it would be that portion of the upper end of the palatoquadrate which comes to articulate with the otic capsule with which the homolog of the hyomandibulare would be joined rather than a point farther down. If, on the other hand, as maintained by Fuchs, the ancestry of the Amphibia is to be sought far back among the primitive elasmobranchs, it is in this region,—over the lateral semicircular canal caudad of the otic articulation of the palatoquadrate,—that the connection of its vestigium might be sought.

One of the characteristics of the urodele stilus is its early connection with the ventral edge of the squamosum, and from the first it has appealed to us as of profound morphological significance. Its final interpretation, however, is not yet possible, and must await the establishment of many facts of relation and development in the domain of comparative morphology. Although from the development of this bone over the lateral semicircular canal in urodeles (Kingsbury '03; Thyng '06) it is regarded by us as a squamosum, other considerations led Gaupp to bestow upon it the indifferent name of *Paraquadratum*. Granting that it is a squamosum, its development requires further study, and its value in urodeles,—as Dermo-, Auto- or Amphisquamosum has to be considered. As an Autosquamosum deriving its cells (primarily?) from the periotic blastema, it may be pointed out that it has precisely the position and relation to the proton of the columella that would be required of it if the hyomandibular homology of the latter is accepted, since in fishes it seems to afford a portion of the articular surface for that bone. Nor do two considerations that immediately occur appear necessarily antagonistic to this view; the first, that in the event of the acceptance of the elasmobranch origin of the Amphibia, no squamosum (as such) existed in the ancestral forms; the second, that the larval connection of the columella with the squamosum is but a step in the shifting of the suspensorium (palatoquadrate) during growth, which in its second phase again transfers the connection to the palatoquadratum or the os quadratum.

The absence of any connection between the columella and the ceratohyal has possibly been most commonly regarded as the greatest defect in the ontogenetic evidence for the hyomandibular homology. Recognition of the existence of a columellar proton outside the otic capsule, its relations to palatoquadrate, otic capsule, and facial nerve, in comparison with the requirement of a first segment of the hyoid arch, renders less important evidence of a connection of ceratohyal and columella. Yet the evidence of an embryological relation of the two structures seems stronger than is usually recognized. Miss Platt ('97), when describing the extra-otic origin of the columella (her operculum) considered that its lack of connection with the

ceratohyal did not "demonstrate that the cartilage in question may not be a rudimentary element of the hyoid arch, since each element of the cartilaginous arches arises from an independent center of chondrification and secondary fusions of cartilaginous elements do not necessarily show original association."

The cord of cells which extends to the under surface of the squamosum and which must be regarded as a part of the columella blastema, is joined by an extension from the perichondral cells of the ceratohyal, so that, at an early stage (19 mm.) the two structures are in fact connected (Kingsbury '03, p. 318, and Fig. 2*a*). In Ambystoma there is a line of cells from the ceratohyal to the columella in the 13-14 mm. specimen. In Plethodon (Text Fig. 6) the juxtaposition is still closer and a cellular continuity exists. In Cryptobranchus the ceratohyal is not joined to the columella by cells in the just hatched larva; just what the condition is at an earlier stage we cannot say from lack of material at a suitable stage.

This early connection by cells does not seem a chance association, but rather to indicate that columella and ceratohyal chondrify out of a common blastema. The Ligamentum hyo-columellare previously described as existing in several forms seems to be a secondary development, though it may express a primitive relationship. The diagram introduced to illustrate the ligaments (Fig. 21) may also serve to indicate the skeletal connections and relations of the columella as a probable hyomandibulare.

The position of the columella above and behind the nervus facialis satisfies the requirements of the hyomandibular homology. It is but necessary to recall its position in elasmobranchs and Polypterus (Ruge '96, Pollard '92) to recognize this fact. No detailed study has been made of the relation of this nerve in fishes, however; nor has the significance of the rather constant position of the columella between the vena petroso-lateralis and the arteria carotis interna been investigated.

The connections and development of the columella do, we believe, strengthen its homology with the Hyomandibulare of fishes, in support of which so much has been written.

Function of the "Sound-Transmitting" Apparatus.

In order to determine the precise function of the so-called sound-transmitting apparatus in Urodeles a series of experiments upon both larvæ and adults is necessary. The skeletal connections of the fenestral elements in the larva, the changes taking place upon the assumption of the terrestrial life and the correlation of structure and habit in certain adults furnishes, however, some basis for judging the function of these structures.

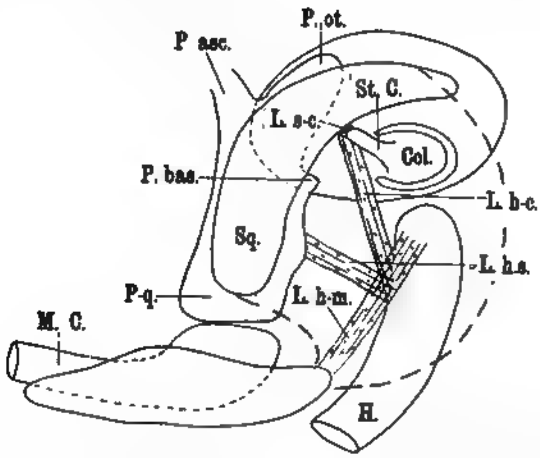


Fig. 21. Schema to illustrate the relation of the ligaments found in this region. *Col.*, columella; *H.*, ceratohyale; *L.h-c.*, ligamentum hyo-columellare; *L.h-m.*, ligamentum hyo-mandibulare; *L.h-s.*, ligamentum hyo-suspensoriale; *L.s-c.*, ligamentum squamoso-columellare; *M.C.*, Meckel's cartilage; *P.asc.*, processus ascendens palatoquadrati; *P. bas.*, processus basalis palatoquadrati; *P.ot.*, processus oticus palatoquadrati; *Pq.*, palatoquadratum; *St.C.*, stilus columellæ; *Sq.*, os squamosum.

It is perhaps not assuming too much to believe that the sound-transmitting apparatus serves as an organ of equilibration and the detection of vibrations of low frequency when such come to the animal through a dense medium such as earth or water. The nature and structure of the apparatus in urodeles seem to preclude the belief that vibrations of any frequency whatsoever can be detected from a medium as rare as the air. There is, however, nothing in the nature of the apparatus to interfere with the view that vibrations

of high frequency are not detected if transmitted to the animal through a dense medium. Experimentation along this line may prove very interesting and valuable.

During the larval period, and in aquatic or partly aquatic forms during adult life, the connection of the fenestral plate is with the suspensorium. Thus it would appear that jars or vibrations are transmitted from the objects, upon which they are resting, to the floor of the mouth, after which the course is through the suspensorium to the columella and thence to the inner ear, as has been

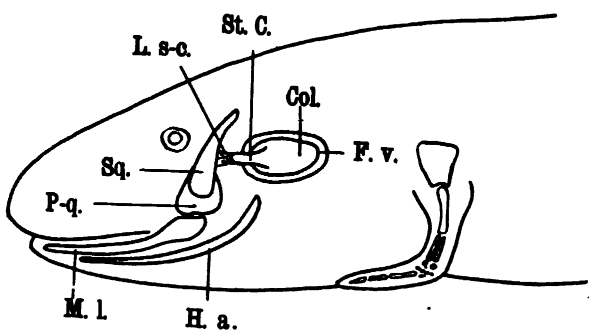


Fig. 21a. Schema to illustrate the possible method of communication between the inner ear and the exterior for larvæ and thoroughly aquatic adult forms. *Col.*, Columella; *F.v.*, fenestra vestibuli; *H.a.*, hyoid arch; *L.s-c.*, ligamentum squamoso-columellare; *M.l.*, skeleton of the lower jaw; *Pq.*, palotoquadratum; *Sp.*, os squamosum; *St.C.*, stilus columellæ.

suggested by Gaupp ('05, '07). The possibility of such a functional mechanism is illustrated in Fig. 21*a*.

At transformation when terrestrial life is assumed, in certain forms, a different type of communication with the exterior is formed. The columella becomes fused with the ear capsule while a free plate, the operculum, is formed behind and below as in Ambystoma or the caudal portion of the fenestral plate remains free as in the Plethodontidæ and some others. This plate is placed in communication with the exterior by the M. opercularis, connecting it with the shoulder girdle. Thus jars and vibrations may be transmitted through the arm to the M. opercularis, thence to the operculum and finally to the inner ear, as shown in Fig. 21 *b*.

These connections appear to be an adaptation to the habits and environment of the animal. During larval life and in such forms as Necturus and Cryptobranchus the body is either supported by water, or rests full length upon the bottom or some submerged object, the arms and legs playing a small part, if any, in its support. The primitive connections of the columella here persist and function as the transmission line between the exterior and the inner ear. Some evidence for this view is found in certain Anurans. In Pelobates there is no tympanic cavity, and the eustachian tube is much reduced. The fenestral plate in this form is connected by strong ligament

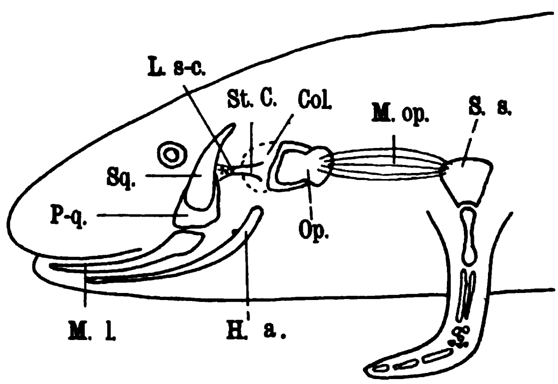


FIG. 21b. Same as Fig. 21a, for terrestrial forms. *Col.*, columella; *H.a.*, hyoid arch; *L.s-c.*, ligamentum squamoso-columellare; *M.op.*, musculus opercularis; *M.l.*, skeleton of lower jaw; *Op.*, operculum; *Pq.*, palatoquadratum; *Sq.*, os squamosum; *S.s.*, suprascapula; *St.C.*, stilus columellae.

with the squamosum. Similar conditions obtain in Bombinator, excepting that the fenestral plate is connected with the hyoid. In either case the inner ear is placed in communication with the exterior through the floor of the mouth. It is interesting to note in this connection that Pelobates is a thoroughly burrowing form while Bombinator is just as thoroughly an aquatic one.

In the urodele Siren, where the usual skeletal connections of the fenestral plate are wanting, they seem to be compensated for by the attachment of the stilus columellæ to the hyoid by means of the strong hyo-columellar ligament.

When terrestrial life is assumed the body is more or less supported

by the limbs, thereby raising the floor of the mouth above the ground. Thus communication of the internal ear with the exterior through the suspensorium and floor of the mouth is lost. By the detachment of a portion of the M. intertransversarius capitis inferior which becomes the M. opecularis, the operculum is connected with the shoulder girdle and communication of the inner ear with the exterior is again established,—through the arm and shoulder girdle.

Summary.

While to a certain extent (hyomandibular homology) comparison has been made with fishes, comparisons between the amphibian auditory apparatus and those of reptiles and mammals have not been attempted. The terms "stapes" and "stapedial" have been purposely avoided since it has seemed to us by no means conclusively shown that the amphibian columella is simply the homolog of the first segment of the mammalian chain of bones. Although we have fully appreciated that this investigation is but a part of the larger problem as was indicated at the beginning of the paper, the main aim has been the determination of *facts* for a large number of tailed amphibians, realizing that weaknesses in broad generalizations are in most instances due to drawing conclusions from insufficient data; for illustration of which it is unnecessary to go outside the limited field of investigation covered by this paper. The amphibian group presents within itself many problems of both local importance and general bearing that require further investigation, and it was this narrower field that particularly engaged our attention. Some of the general aspects of the problem we hope to deal with subsequently.

The main results were given in the first portion of the paper; they are restated below in somewhat extended form.

1. Several (4 to 7) different types of "columella auris" are found in urodeles.

2. There are two morphologically distinct fenestral structures found in the group: Columella and Operculum.

3. The Columella possesses a stilus, tends to fuse with the cephalic portion of the fenestral margin, and in ontogeny seems to come from outside the otic capsule.

4. The Operculum develops out of the otic capsule of which it appears to be primarily a part. It possesses no stilus but gives attachment to a muscle (M. opercularis). Its morphological position relative to the Columella is caudal and medial.

5. A Columella only is present in Necturus, Proteus, Cryptobranchus, Amphiuma, Siren.

6. In Ambystoma and Chondrotus (Ambystomidæ) a Columella is present in the larva but it becomes fused with the otic capsule at transformation, and an Operculum is then developed.

7. A vestigial and fused Columella is found in Salamandra, Triton and Diemictylus (Salamandridæ, Pleurodelidæ, Cope).

8. An Operculum is found (in the adult) in the Ambystomidæ, Salamandridæ, Pleurodelidæ.

9. The Plethodontidæ and Desmognathidæ possess a single fenestral structure bearing a stilus but also giving attachment of the opercular muscle.

10. Typhlomolge possesses a fenestral plate of plethodontid character. It has a fragmented stilus and lacks the M. opercularis.

11. The Musculus opercularis is absent in (a) Necturus, Proteus, Cryptobranchus, Amphiuma, Siren, Typhlomolge; (b) in larvæ generally. It is present in the adult Ambystomidæ, Salamandridæ, Pleurodelidæ, Plethodontidæ, and Desmognathidæ.

12. The Stilus columellæ is distally joined to the Squamosum, Palatoquadratum, Quadratum, singly or in combination. In Necturus, Proteus, Cryptobranchus, Typhlomolge and larvæ generally (Ambystomidæ, Plethodontidæ, Desmognathidæ) it is directly connected with the squamosum.

13. During growth or at transformation the connection tends to shift, usually to the Palatoquadratum.

14. The stilus is fragmented in Typhlomolge, vestigial in Batracoseps and Siren, absent in Triton and Diemictylus. In Salamandra its distal end is fused with the Palatoquadratum.

15. In development the proton of the Columella appears to be outside the otic capsule in those forms in which its development has been traced (Necturus, Ambystoma, Spelerpes, Plethodon, Cryptobranchus).

16. The proton of the Columella is connected by a distinct strand of cells with a group of cells between Squamosum, Processus oticus palatoquadrati and the Prominentia semicircularis lateralis of the otic capsule.

17. The facial nerve is entirely below the Columella (stilus columellæ) in all forms except Necturus, Proteus, Typhlomolge; in these, one ramus (R. jugularis) passes above the stilus.

18. The relation of the stilus to the blood vessels of the otic region appears quite characteristic; i. e., below the vein and above the artery.

19. A Ligamentum hyo-columellare is present in Siren, Amphiuma, Cryptobranchus, Desmognathus and many Plethodontidæ.

20. The hyomandibular homology is favorably discussed.

21. The homology of the Columella of Urodela and the Pars interna plectri of Anura is accepted.

22. The Operculum is regarded as a secondary development in those forms which possess it.

23. From the standpoint of functional adaptation, there seem to be in the Urodela three types of communication of the internal ear with the exterior: (a) through the floor of the mouth, mandible, suspensorium and columella; (b) through the floor of the mouth, the hyoid arch and columella; (c) through the manus, pectoral girdle, M. opercularis and operculum.

24. Type (a) is the more usual and is found in typically aquatic forms. Type (b) is best represented in Siren. Type (c) occurs in Salamandra, Triton and Diemictylus. A combination of (a), (b), and (c) is found in the Plethodontidæ and Desmognathidæ.

25. There appears a close correlation of the type present and the habits of the form (aquatic, semi-aquatic, terrestrial, burrowing, etc.).

Cornell University,
Ithaca, N. Y., June 22, 1909.

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ABBREVIATIONS.

A. General Skeleton.

Col., columella.
H., ceratohyale.
H.a., Hyoid arch.
M.C., Meckel's cartilage.
M.l., Skeleton of lower jaw.
Op., Operculum.
Parasphen., os parasphenoideum.
P.asc., Processus ascendens palatoquadrati.
P.bas., processus basalis palatoquadrati.
P.ot., processus oticus palatoquadrati.
P.h-p., processus hyoideus palatoquadrati.
P-q., palatoquadratum.
Pt., os pterygoideum.
Q., os quadratum.
S.s., Suprascapula.
St.C., stilus columellae.
Sq., os squamosum.

B. Ear Capsule.

C.l., Canalis semicircularis lateralis.
C.p., cavum perilymphaticum.
Cr.s., crista semicircularis.
D.p., ductus perilymphaticus.
"F", secondary fenestra vestibuli.
F.p., fenestral plate.
F.v., fenestra vestibuli.
L., lagena.
Prom. l., prominentia semicircularis lateralis.
Prom.p., prominentia perilymphatica.
R.p., recessus perilymphaticus.

C. Ligaments.

L.h-c., ligamentum hyo-columellare.
L.h-m., ligamentum hyo-mandibulare.
L.h-s., ligamentum hyo-suspensoriale.
L.s-c., ligamentum squamoso-columellare.

D. Nerves.

VII, nervus facialis (VII).
R.h.VII, ramus hyomandibularis VII.
R.c., ramus communicans (IX-VII).
R.j.VII, ramus jugularis VII.
R.m.e.VII, ramus mandibularis externus VII.
R.m.i.VII, ramus mandibularis internus VII.

E. Muscles.

M., musculus cephalo-dorso-mandibularis.
M.op., musculus opercularis.
M.i.c.i., musculus intertransversarius capitis inferior.

F. Blood Vessels.

C., arteria carotis interna.
V.p.-l., vena petroso-lateralis.

PLATE I.

Models of the ear region of the skull of Ambystoma punctatum, drawn from the side and slightly from the caudal and ventral aspects.

Fig. 22. Ambystoma punctatum, mature larva about 45 mm. in length, beginning transformation, gills about one-half absorbed.

Fig. 23. Ambystoma punctatum, about 42 mm. in length, transformation period, gills mere stumps. In comparison with Fig. 22, there is shown the partially formed operculum with the opercular muscle.

Fig. 24. Ambystoma punctatum, young adult, about 52 mm. in length. The columella is now nearly completely fused. Remnants of the secondary fenestra are marked "F." Operculum and opercular muscle.

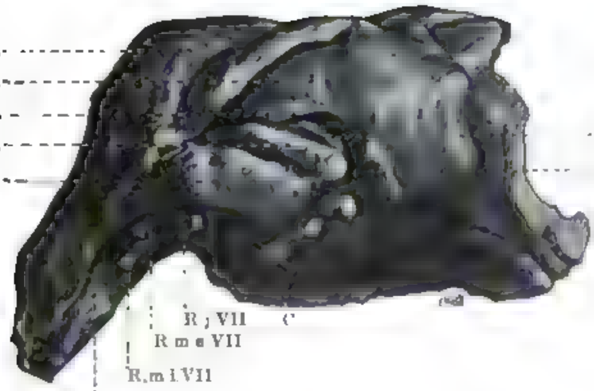

FIG. 22.

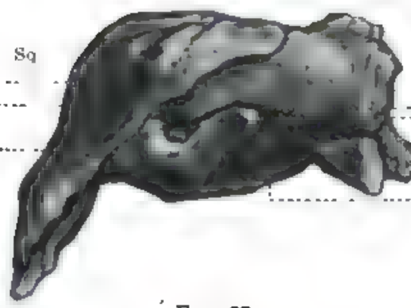

FIG. 23.

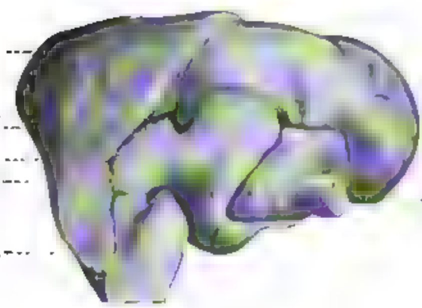

FIG. 24.

PLATE II.

Drawings of models of the ear region of the skull.

Fig. 25. Ambystoma punctatum, adult. A portion of the ear region of the skull showing the completely fused columella and the fully formed operculum with its attached muscle.

Fig. 26. Salamandra maculosa, adult. The region and aspect as in Fig. 25 with which it may be directly compared. The boundary between muscle and operculum is indicated by the broken line.

Fig. 27. Triton cristatus, larva 34 mm. long. The ventro-lateral aspect of the cartilaginous ear capsule. The cephalic part of the fenestra is occupied by the small and partially fused columella above, a growth of cartilage below. The operculum is still broadly joined to the ear capsule.

Fig. 28. Typhlomolge rathbuni, adult. Lateral aspect of the ear region. Attention is particularly called to the segmented (fragmented) stilus columellæ and its relation to the facial nerve (ramus jugularis).

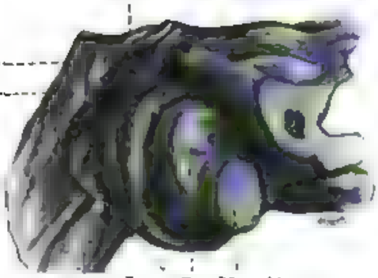

FIG. 25.

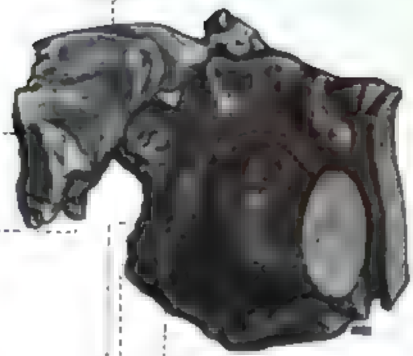

FIG. 26.

FIG. 27.

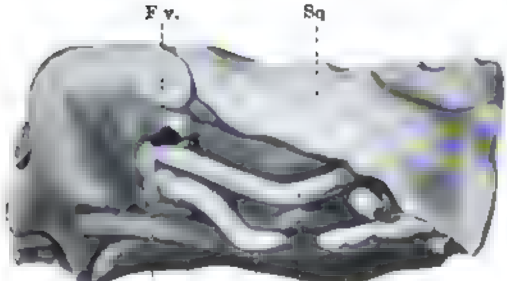

FIG. 28.

EXPLANATION OF PLATES III-IX.

A series of microphotographs to illustrate particularly the morphological relations of columella and operculum, from sections through the ear region.

PLATE III.

Fig. 29. Ambystoma punctatum, adult. Section through the stilus columellae, showing the columellar ligament and its relation to vein and facial nerve.

FIG. 30. The same. Section farther caudad. The fused columella is external to the cephalic end of the operculum.

Fig. 31. Ambystoma punctatum, larva, early transformation. There is shown columella and the floor of the ear capsule to become operculum. Compare with Fig. 32.

Fig. 32. Ambystoma punctatum, transformation period. The operculum is, at this level, separated from the floor of the ear capsule.

Fig. 33. Ambystoma punctatum, larva, 35 mm. in length. It shows the columella, stilus, squamoso-columellar ligament. Note the relation of the vein and artery in this and the two preceding figures.

Fig. 34. Chondrotus tenebrosus, larva. Note the massive stilus articulating with the squamosum and its relation to artery, vein and nerve.

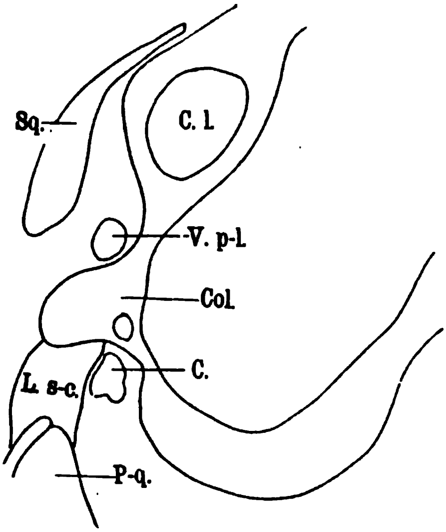

FIG. 29.—Adult Ambystoma.

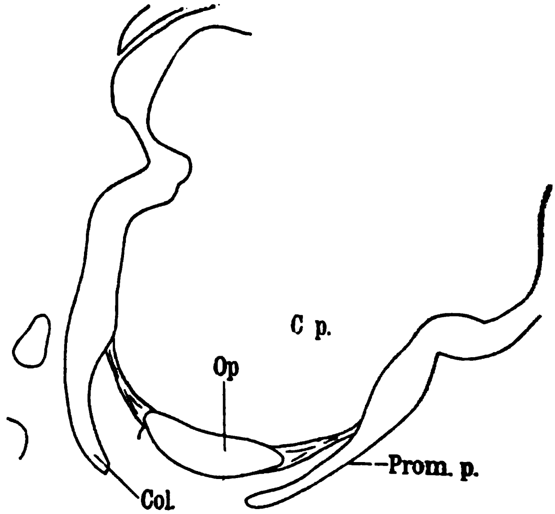

FIG. 30.—Adult Ambystoma.

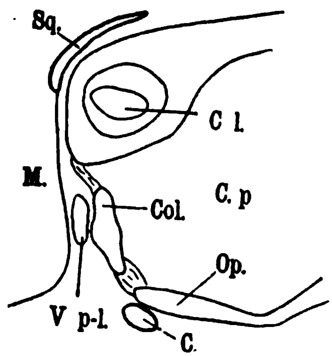

FIG. 31.—Larval Ambystoma.

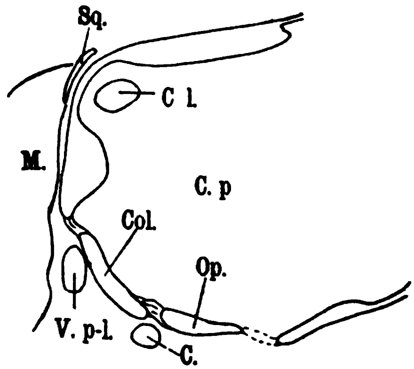

FIG. 32.—Larval Ambystoma.

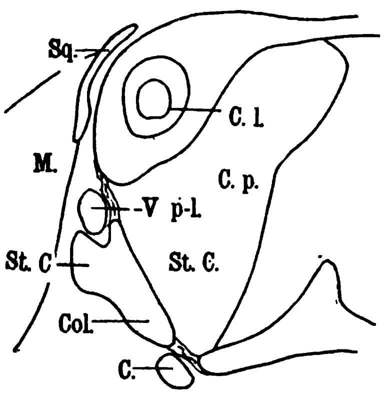

FIG. 33.—Larval Ambystoma.

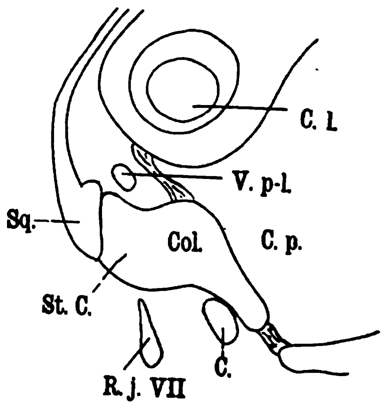

FIG. 34.—Larval Chondrotus.

FIG. 29.—Adult Ambystoma.

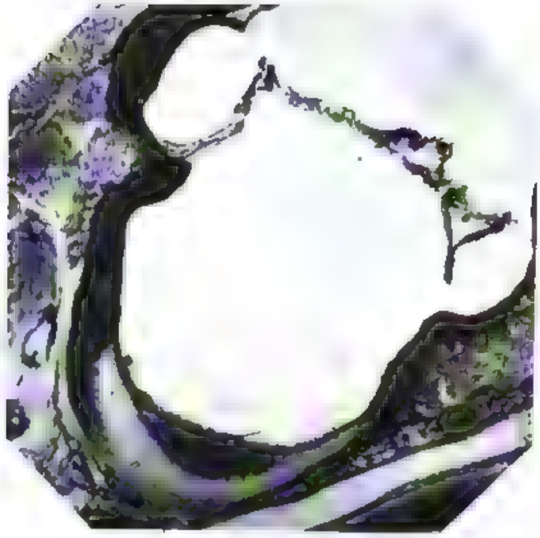

FIG. 30.—Adult Ambystoma.

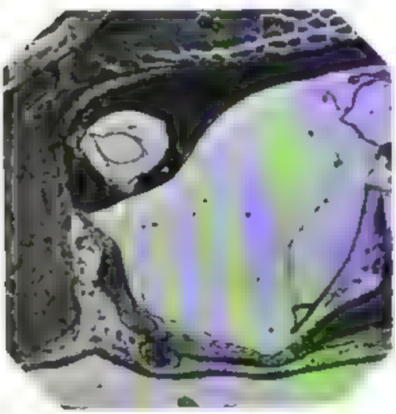

FIG. 31.—Larval Ambystoma.

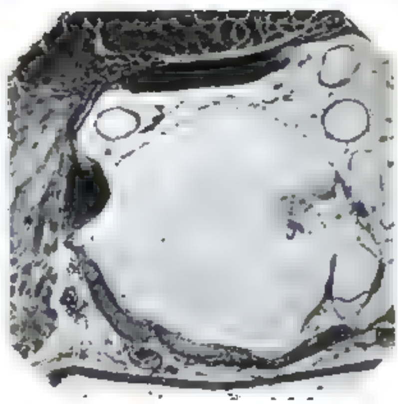

FIG. 32.—Larval Ambystoma.

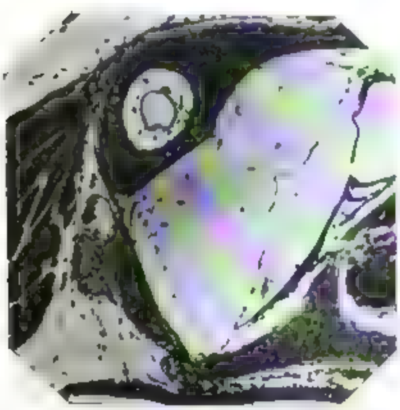

FIG. 33.—Larval Ambystoma.

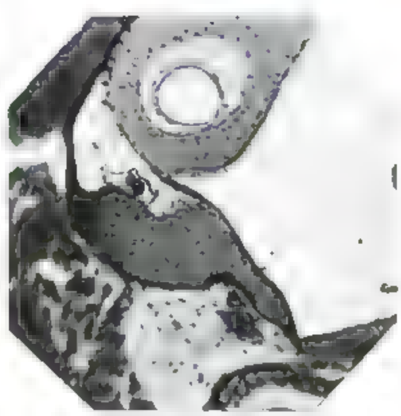

FIG. 34.—Larval Chondrotus.

Plate IV.

Fig. 35. Ambystoma punctatum, adult. Section farther caudad than Fig. 30. Operculum, opercular muscle and recessus perilymphaticus are shown.

Fig. 36. Chondrotus tenebrosus, transformation period. Section through stilus columellæ and the cephalic end of the developing operculum.

Fig. 37. Ambystoma punctatum, transforming. Horizontal section showing columella, stilus, squamoso-columellar ligament, the developing operculum and the M. opercularis attached in front to the opercular plate and behind to the suprascapula.

Fig. 38. Chondrotus tenebrosus, transformation period. Section farther caudad than Fig. 36. It shows the columella. The operculum is partially cut out from the floor of the ear capsule.

Fig. 39. Ambystoma punctatum, embryo 13-14 mm. in length. The columella consists of a mass of cells against the membrane of the fenestra and connected by a strand of dense tissue with the cells upon the prominence of the lateral semicircular canal. Above the columellar proton is the vena petroso-lateralis; below, the carotid artery.

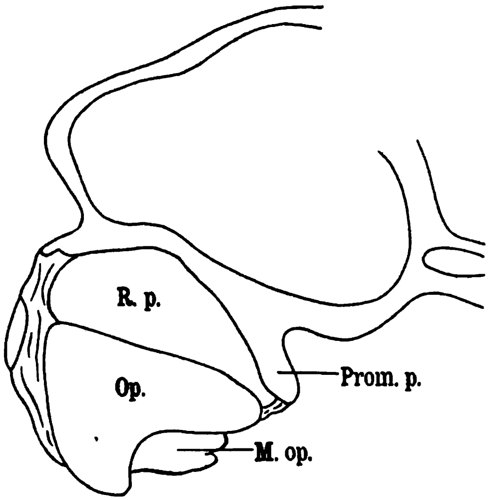

FIG. 35.—Adult Ambystoma.

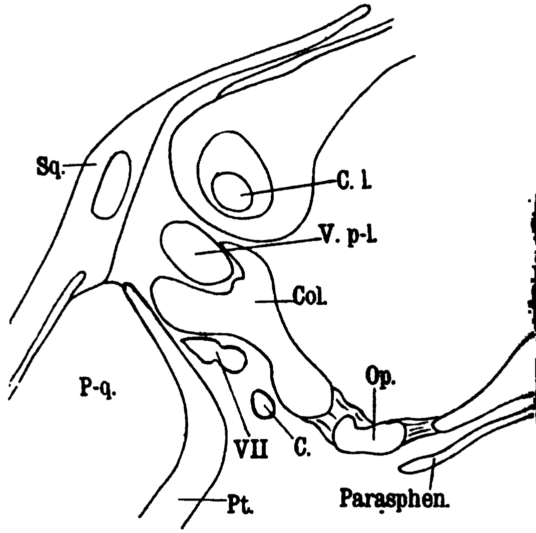

FIG. 36.—Transforming Chondrotus.

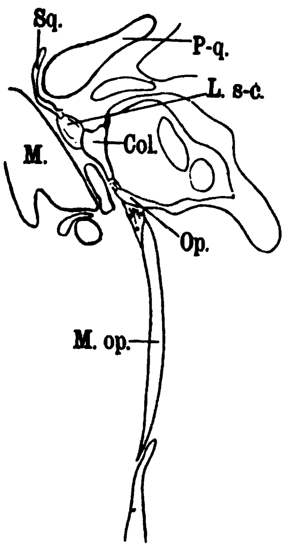

FIG. 37.
Transforming Ambystoma.

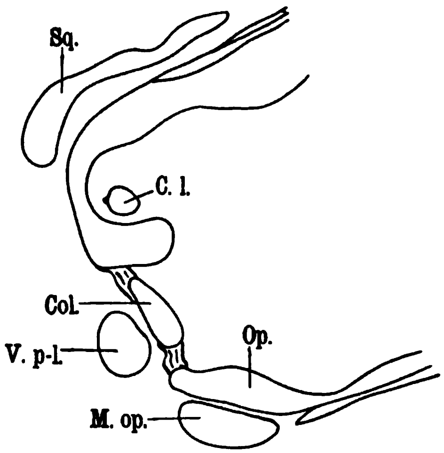

FIG. 38.—Transforming Chondrotus.

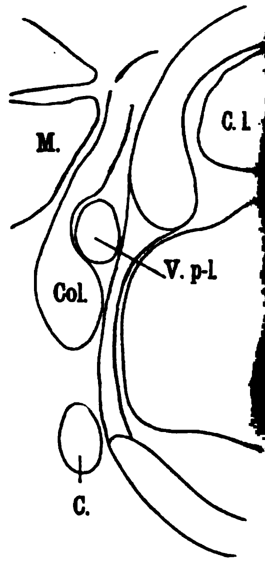

FIG. 39.
Embryo Ambystoma.

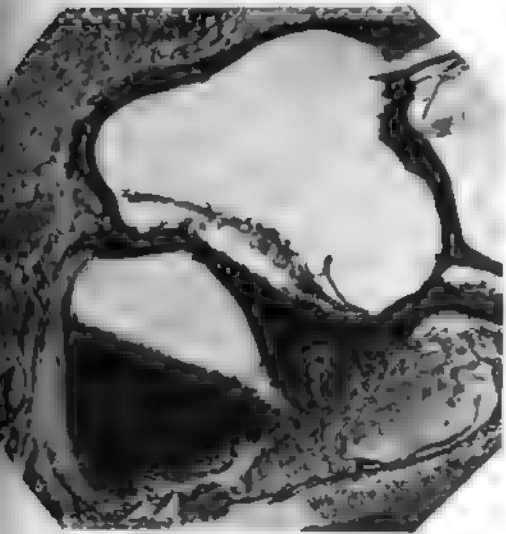

FIG. 35. Adult Ambystoma.

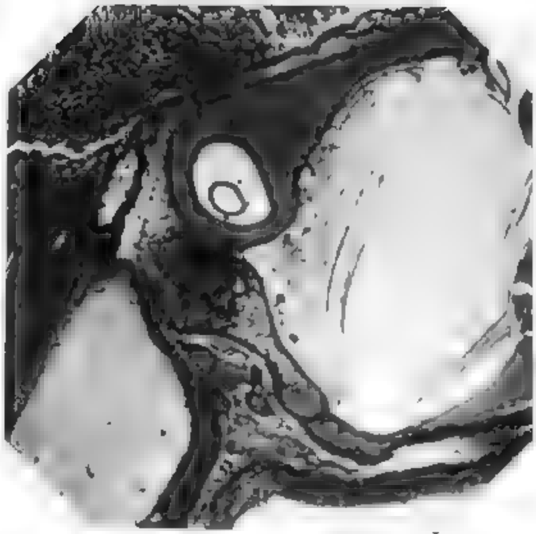

FIG. 36.—Transforming Chondrotus.

FIG. 37.
Transforming Ambystoma.

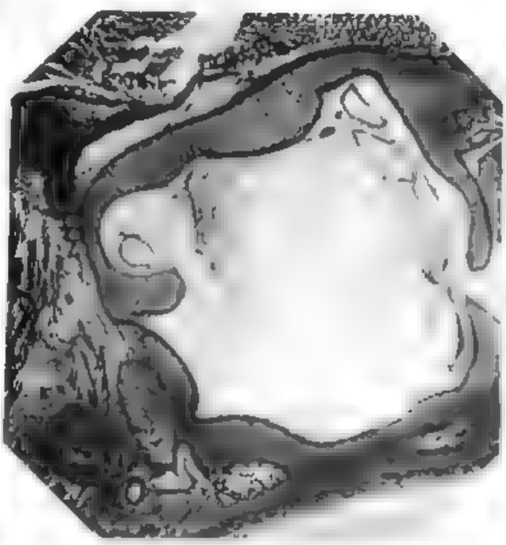

FIG. 38.—Transforming Chondrotus.

FIG. 39.
Embryo Ambystoma.

PLATE V.

Fig. 40. Salamandra maculosa, adult. Section through the stilus columellæ which is continuous with the palatoquadrate.

Fig. 41. The same. Section farther caudad, through the cephalic end of the operculum.

Fig. 42. The same. Section farther caudad through the operculum and the recessus. The M. opercularis would be shown in a section farther caudad.

Fig. 43. Triton cristatus, adult. Section through the cephalic portion of the operculum.

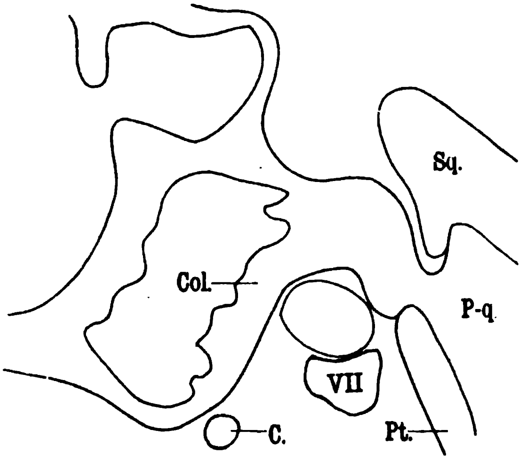

Fig. 40.—Adult Salamandra.

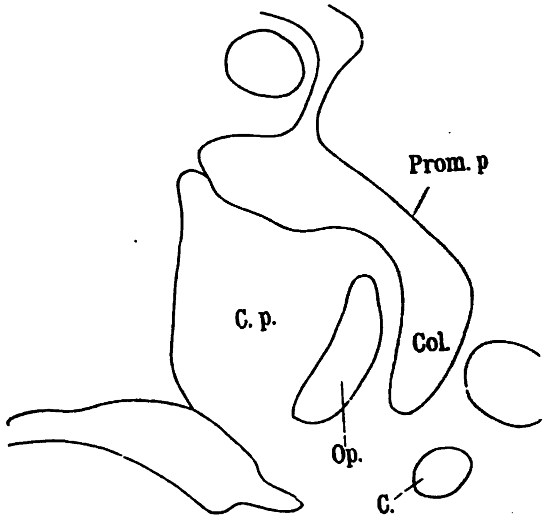

Fig. 41.—Adult Salamandra.

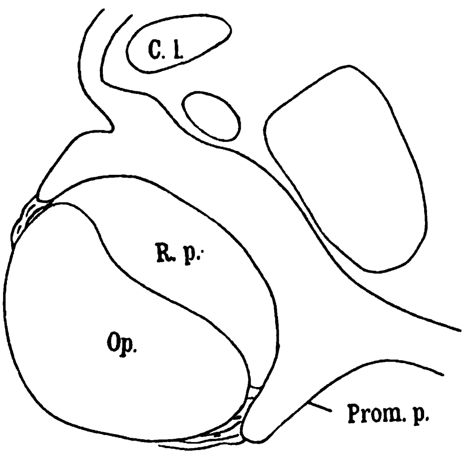

Fig. 42.—Adult Salamandra.

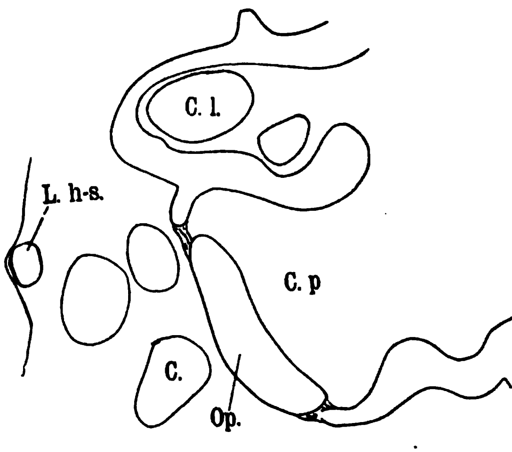

Fig. 43.—Adult Triton.

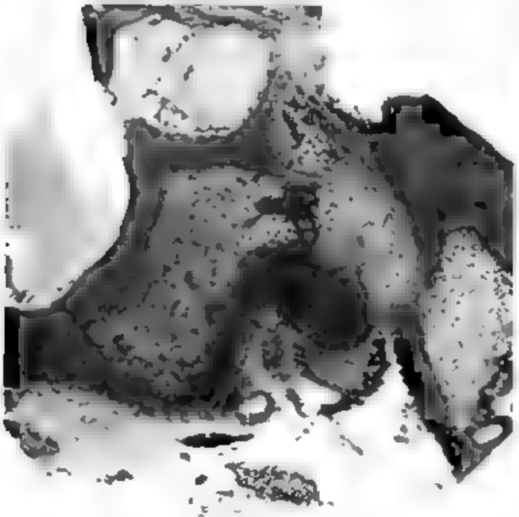

Fig. 40. Adult Salamandra.

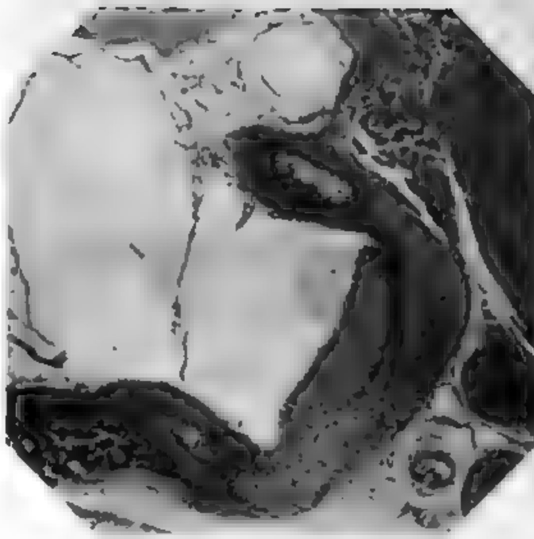

Fig. 41.—Adult Salamandra.

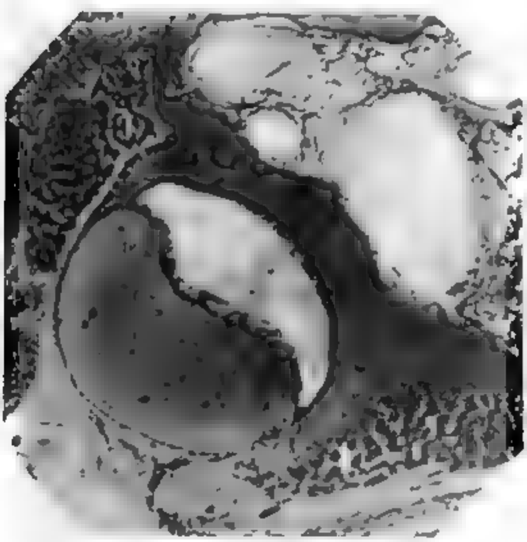

Fig. 42.—Adult Salamandra.

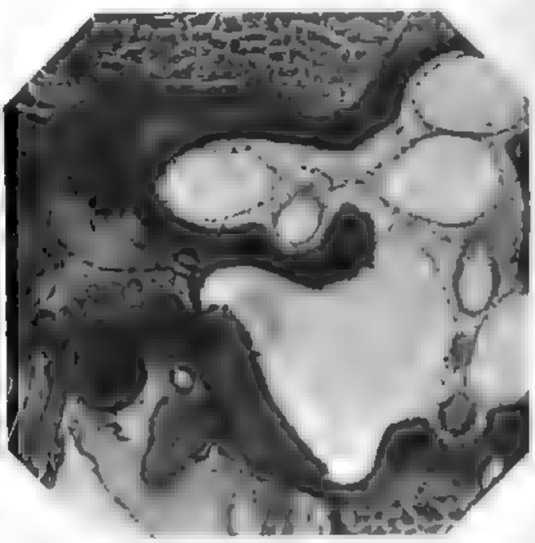

Fig. 43. Adult Triton

Plate VI.

Fig. 44. The same. Section farther caudad, showing the operculum, M. opercularis and recessus perilymphaticus.

Fig. 45. Gyrinophilus porphyriticus, adult. Section through the cephalic end of the fenestra vestibuli and the distal end of the stilus columellæ showing its articulation. Note the relation of blood vessels and facial nerve.

Fig. 46. The same. Section through the base of the stilus, a few sections farther caudad.

Fig. 47. The same. Several sections farther caudad, through the caudal portion of the fenestral plate, opercular muscle and recessus.

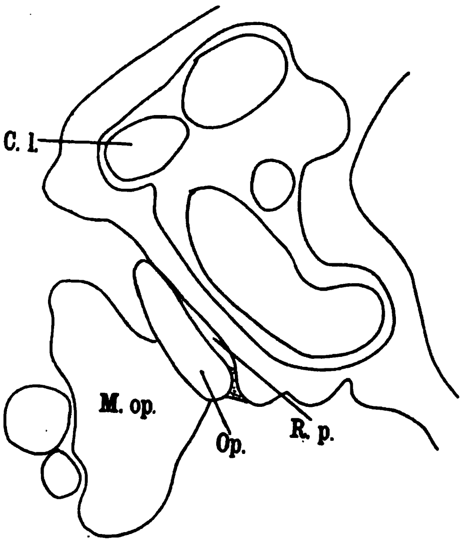

FIG. 44.—Adult Triton.

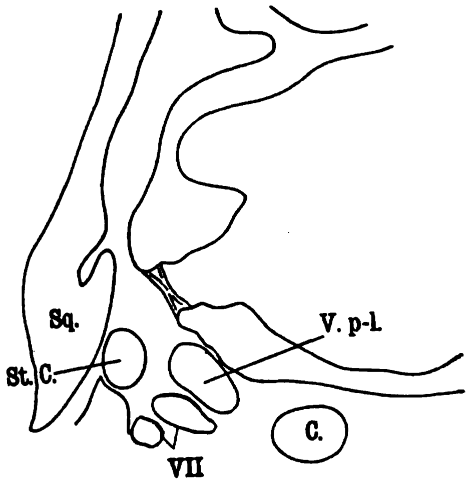

FIG. 45.—Adult Gyrinophilus.

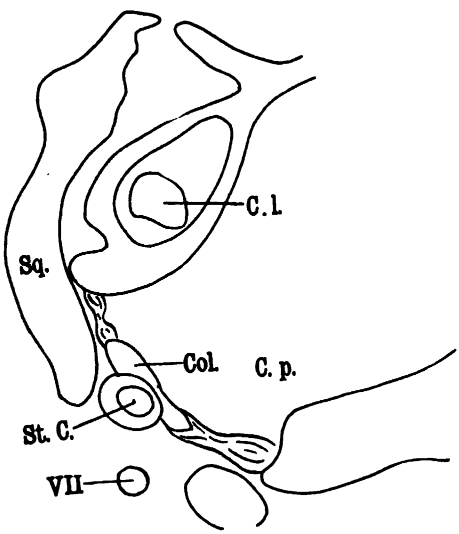

FIG. 46.—Adult Gyrinophilus.

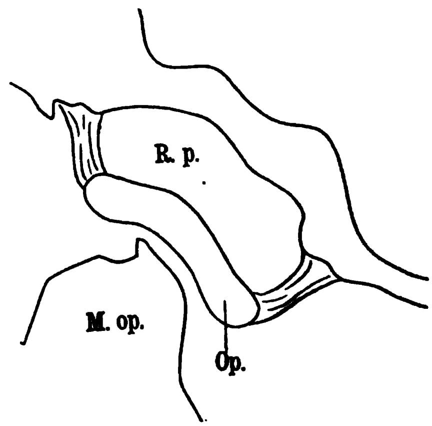

FIG. 47.—Adult Gyrinophilus.

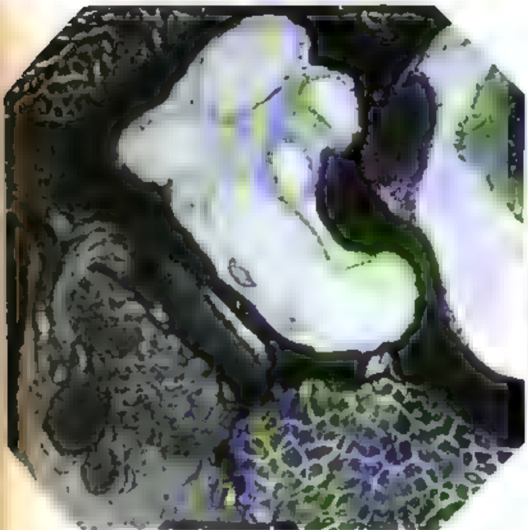

FIG. 44.—Adult Triton.

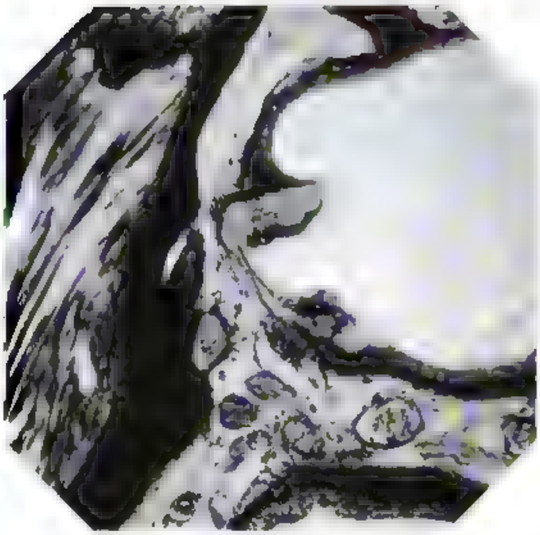

FIG. 45.—Adult Gyrinophilus.

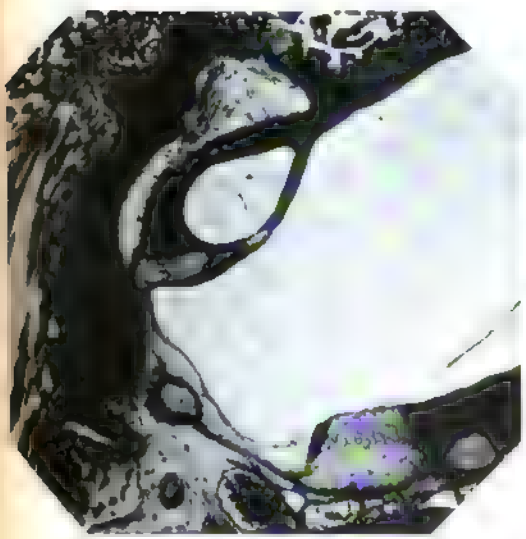

FIG. 46.—Adult Gyrinophilus.

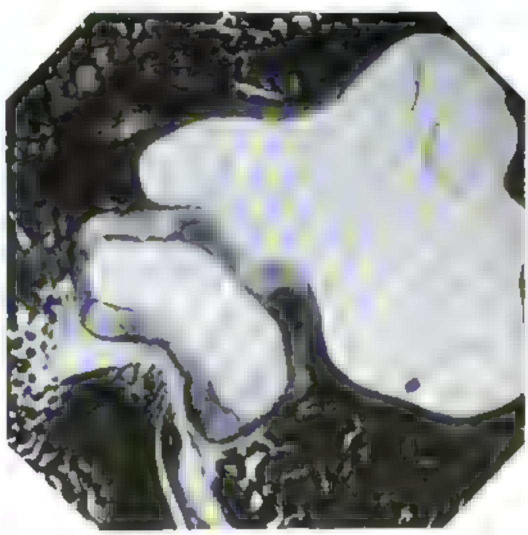

FIG. 47.—Adult Gyrinophilus.

Plate VII.

Fig. 48. Triton cristatus, larva 36 mm. long. The section is through the cephalic end of the columella where it is continuous with the ear capsule on its medial side.

Fig. 49. The same, farther caudad, through the columella and just in front of the cephalic end of the operculum.

Fig. 50. The same. A section still farther caudad, through the operculum and back of the caudal end of the columella. Note the relations of the blood vessels in this and the two preceding figures.

Fig. 51. Cryptobranchus allegheniensis, larva 34 mm. long. The ligamentum hyo-columellare is just joining the stilus at its bend.

Fig. 52. Crytobranchus allegheniensis. Just hatched larva. The proton of the columella is seen between the artery and vein.

Fig. 53. The same. A section farther cephalad to show the proton of the squamosal connection of the columella.

Fig. 54. Cryptobranchus allegheniensis, adult. A section through the distal end of the stilus to show its articulation.

Fig. 55. The same. A section farther caudad showing the columella and its large stilus illustrating the relation to artery, vein and nerve.

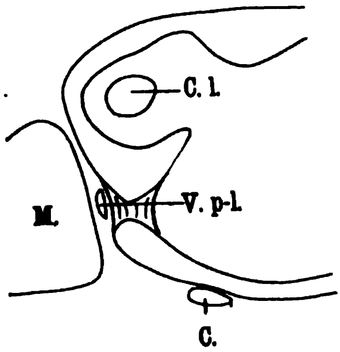

Fig. 48.—Larval Triton.

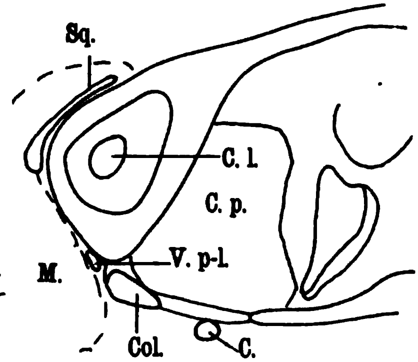

Fig. 49.—Larval Triton.

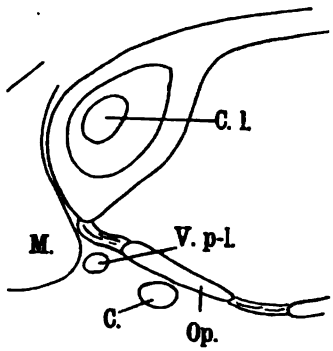

Fig. 50.—Larval Triton.

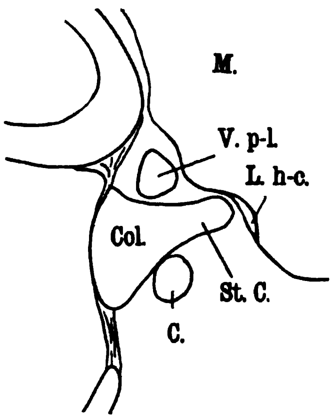

Fig. 51.
Larval Cryptobranchus.

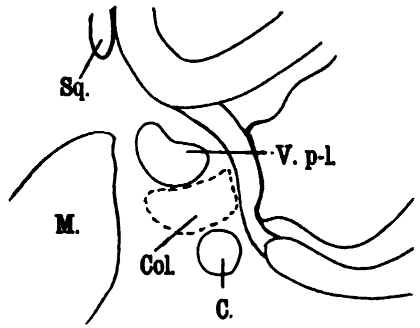

Fig. 52.—Just hatched Cryptobranchus.

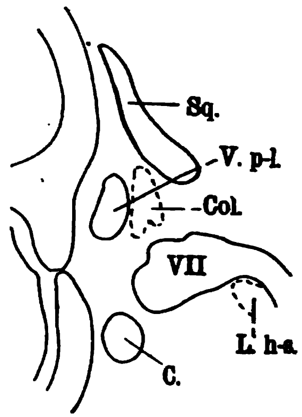

Fig. 53.
Just hatched Cryptobranchus.

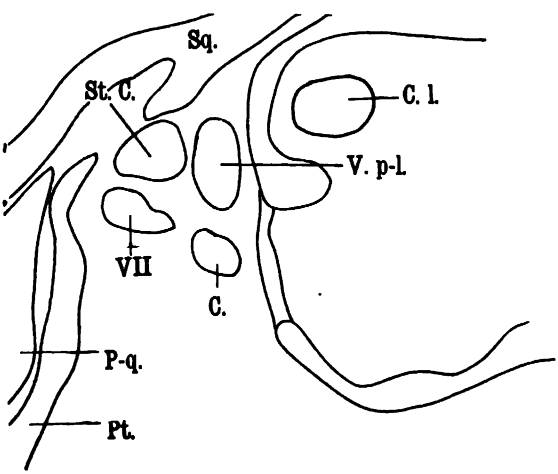

Fig. 54.—Adult Cryptobranchus.

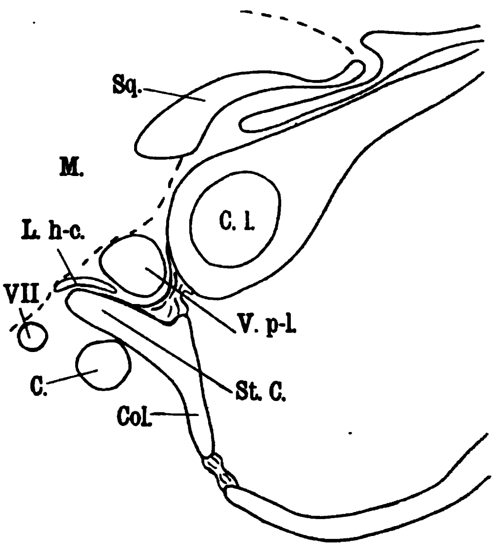

Fig. 55.—Adult Cryptobranchus.

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FIG. 48.—Larval Triton.

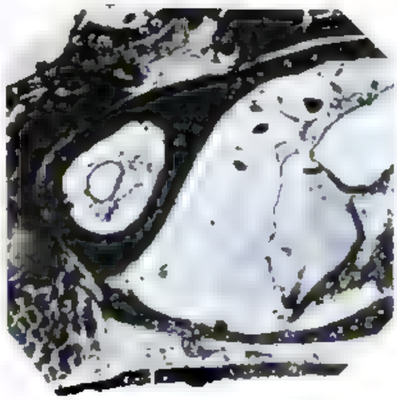

FIG. 49.—Larval Triton.

FIG. 50.—Larval Triton

FIG. 51.
Larval Cryptobranchus.

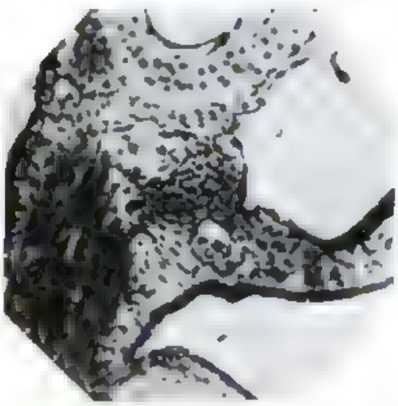

FIG. 52.—Just hatched Cryptobranchus.

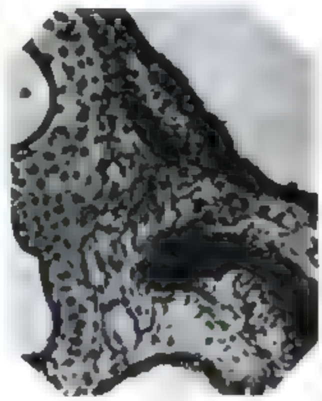

FIG. 53.
Just hatched Cryptobranchus.

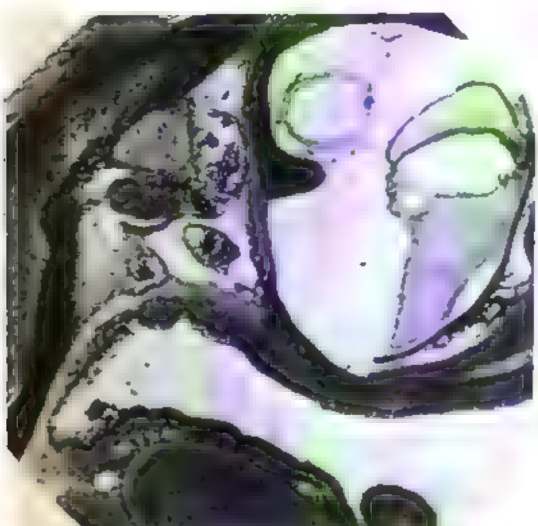

FIG. 54.—Adult Cryptobranchus.

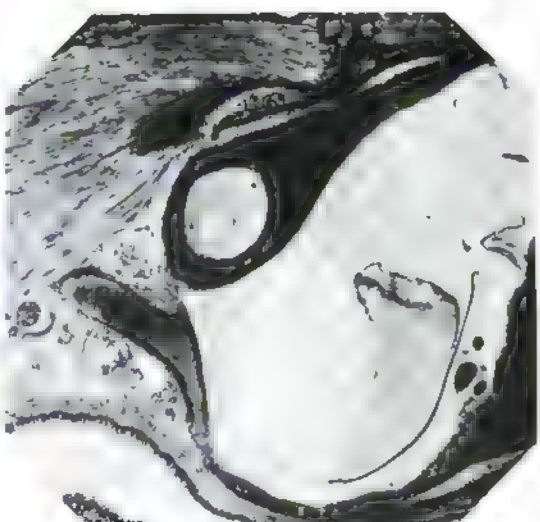

FIG. 55.—Adult Cryptobranchus.

Plate VIII.

Fig. 56. The same. A few sections farther caudad through the caudal portion of the fenestral plate.

Fig. 57. Necturus maculosus, larva. The ligamentum squamoso-columellare is just attaching to the ventral edge of the squamosum.

Fig. 58. The same, a few sections farther caudad. The ramus jugularis VII is shown passing over the ligament.

Fig. 59. The same, still farther caudad through the base of the stilus columellæ. Note the relations of artery, vein and nerve in this and the two preceding figures.

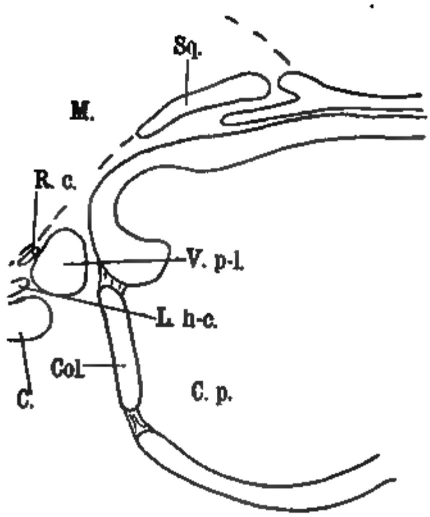

Fig. 56.—Adult Cryptobranchus.

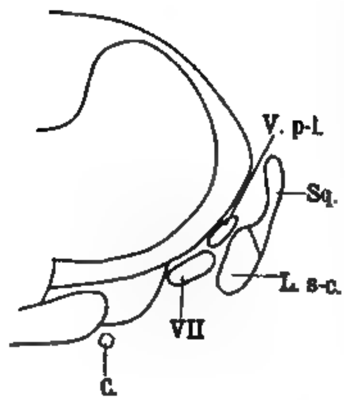

Fig. 57.—Larval Necturus.

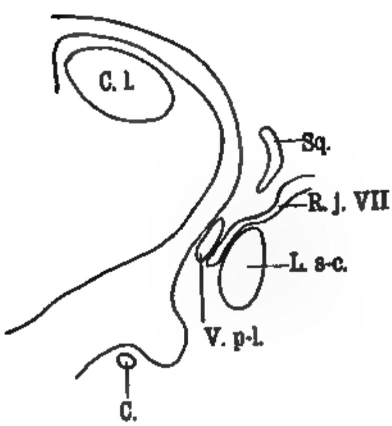

Fig. 58.—Larval Necturus.

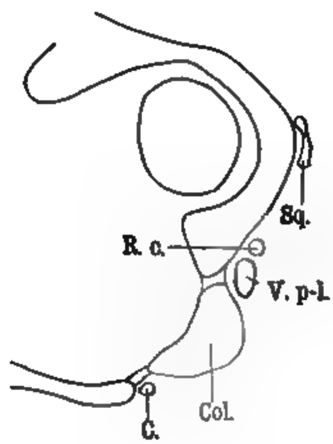

Fig. 59.—Larval Necturus.

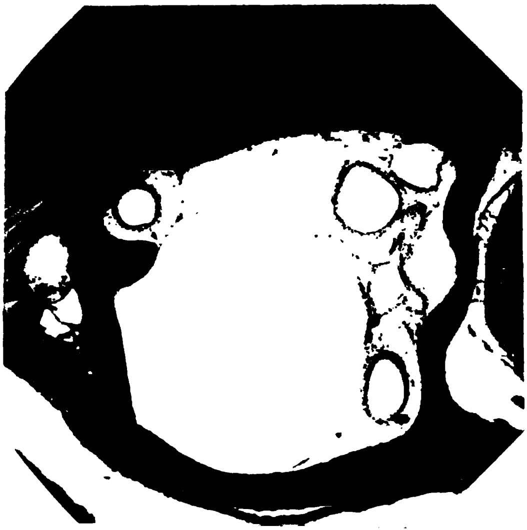

Fig. 56.—Adult Cryptobranchus.

Fig. 57.—Larval Necturus.

Fig. 58.—Larval Necturus.

Fig. 59.—Larval Necturus.

PLATE IX.

Fig. 60. The same, still farther caudad, showing the caudal portion of the fenestral plate of the columella with its inner and outer bony plates.

Fig. 61. Siren lacertina, adult. Section showing the columella, ceratohyale the hyo-columellar ligament, into which projects the short stilus, and the cartilaginous portion of the ear capsule that forms the perilymphatic prominence.

Fig. 62. The same, a few sections farther caudad. The caudal end of the stilus is in the ligament. The perilymphatic prominence; position of artery and vein.

Fig. 63. The same, farther caudad behind the fenestra and showing the caudal portion of the perilymphatic prominence.

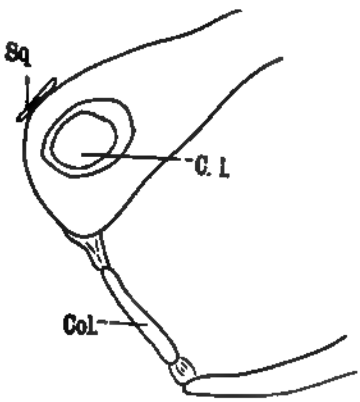

Fig. 60.—Larval Necturus.

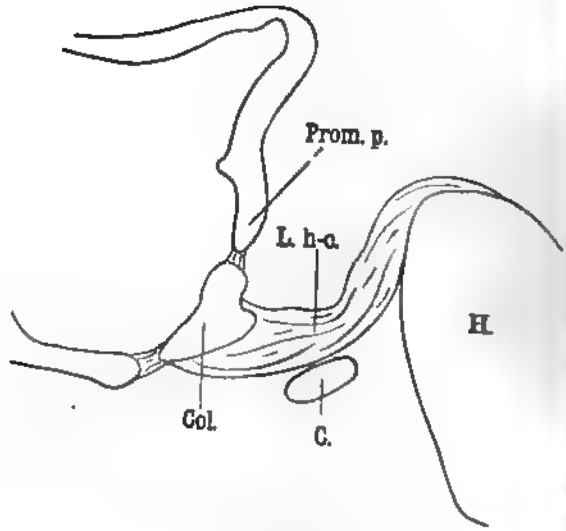

Fig. 61.—Adult Siren.

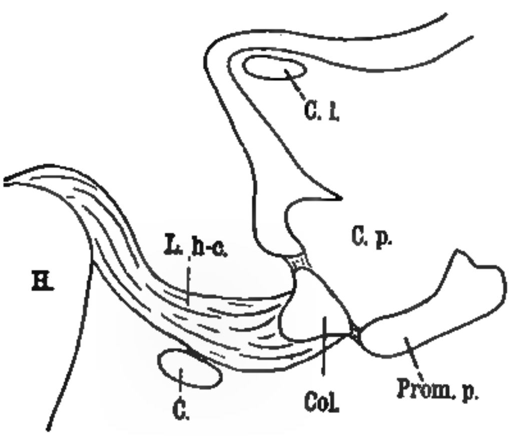

Fig. 62.—Adult Siren.

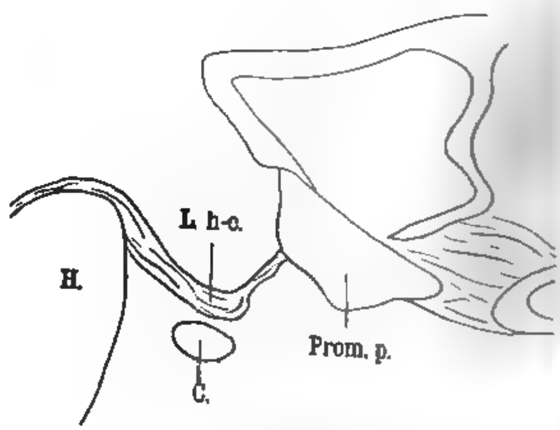

Fig. 63.—Adult Siren.

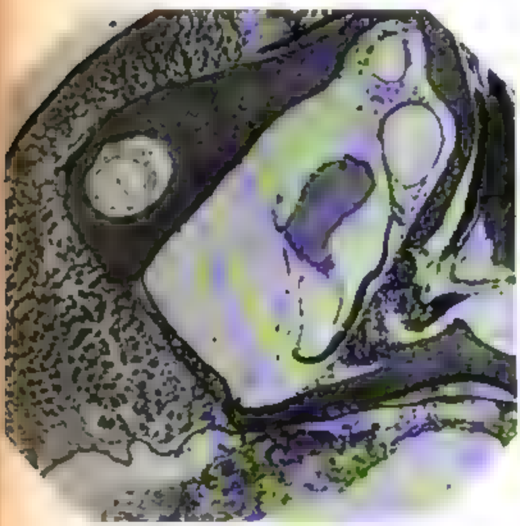

FIG. 60.—Larval Necturus.

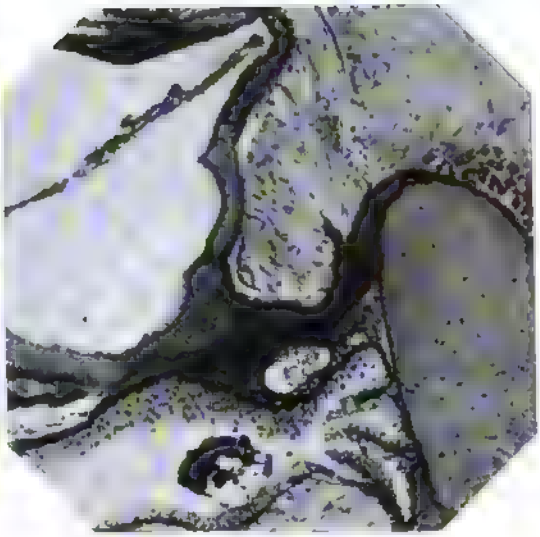

FIG. 61.—Adult Siren

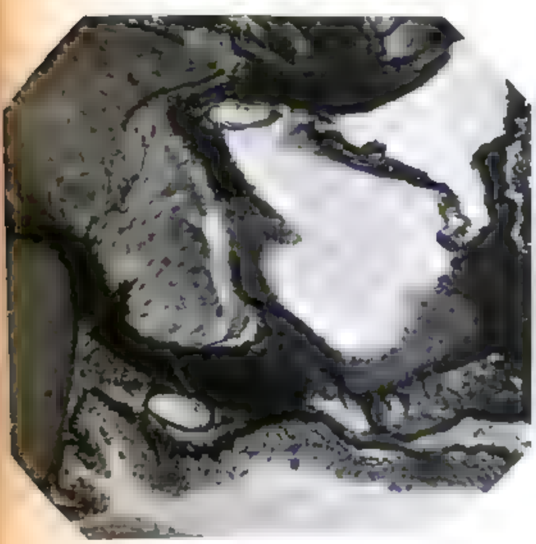

FIG. 62.—Adult Siren

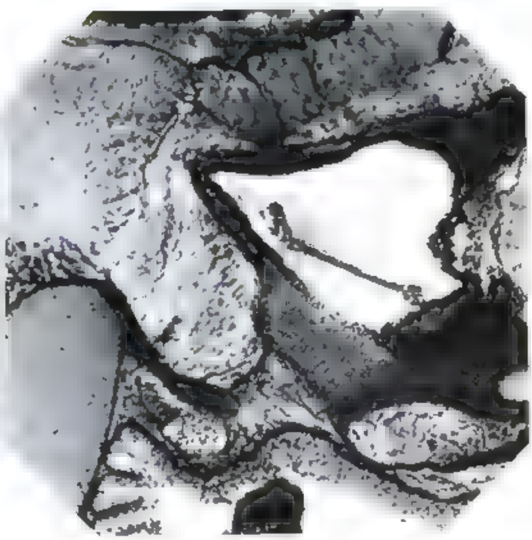

FIG. 63.—Adult Siren

Plate X.

(Figures 64-72)

A series of schemas showing the number and relative position of the elements present in the fenestra vestibuli in the various groups of the tailed Amphibia, together with the relation of these elements to the ear capsule, suspensorium, hyoid arch, M. opercularis, and facial nerve. It should be stated that they are to show relations only; the representation of the processes of the palatoquadrate, for example, being purely diagrammatic. In Fig. 67 the relation of the hyoid arch (H.) is intended to represent the condition in certain forms only.

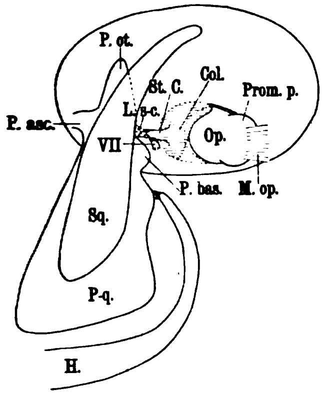

FIG. 64.—Ambystoma.

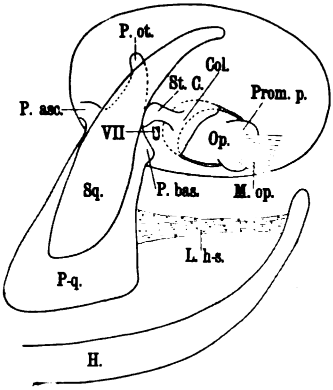

FIG. 65.—Salamandra

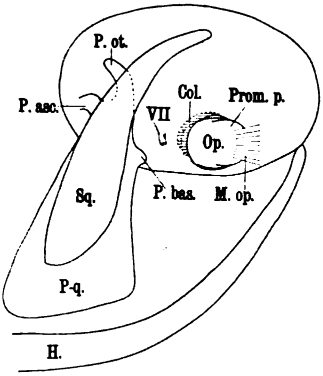

FIG. 66.—Triton and Diemictylus.

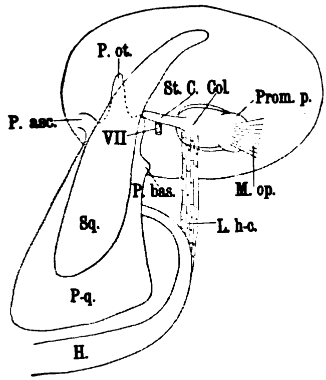

FIG. 67.—Plethodontidæ and Desmognathidæ.

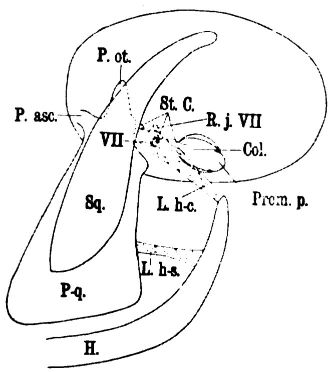

FIG. 68.—Typhlomolge.

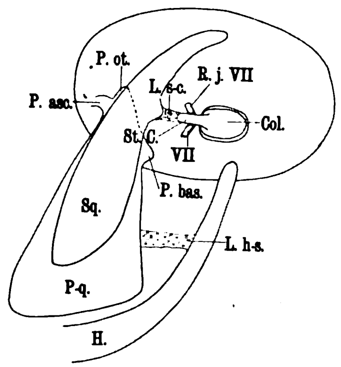

FIG. 69.—Necturus.

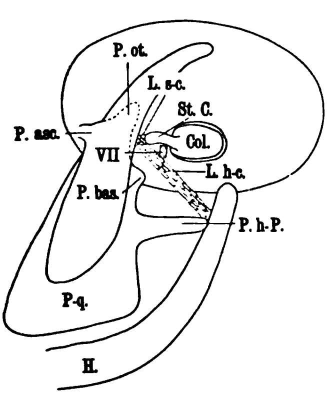

FIG. 70.—Cryptobranchus.

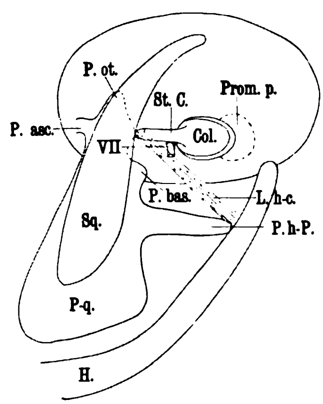

FIG. 71.—Amphiuma.

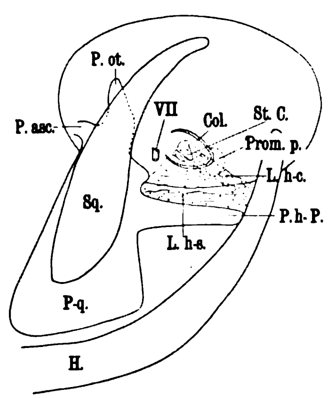

FIG. 72.—Siren.

With the Author's Compliments

THE HYO-BRANCHIAL APPARATUS OF TYPHLO-TRITON SPELÆUS STEJN

WILLIAM A. HILTON, PH.D.

[Reprinted from BIOLOGICAL BULLETIN, Vol. XVI., No. 4, March, 1909.]

THE HYO-BRANCHIAL APPARATUS OF TYPHLOTRITON SPELÆUS STEJN.

WILLIAM A. HILTON, PH.D.

The cave salamander *Typhlotriton* was put in the family Desmognathidæ by Stejneger, in 1892.[1] The basis of this classification was chiefly certain skeletal characters, such as the structure of the vertebræ. The study of the hyo-branchial apparatus of this form seems to show other relationships.

In the larvæ of *Typhlotriton*, which are often found almost

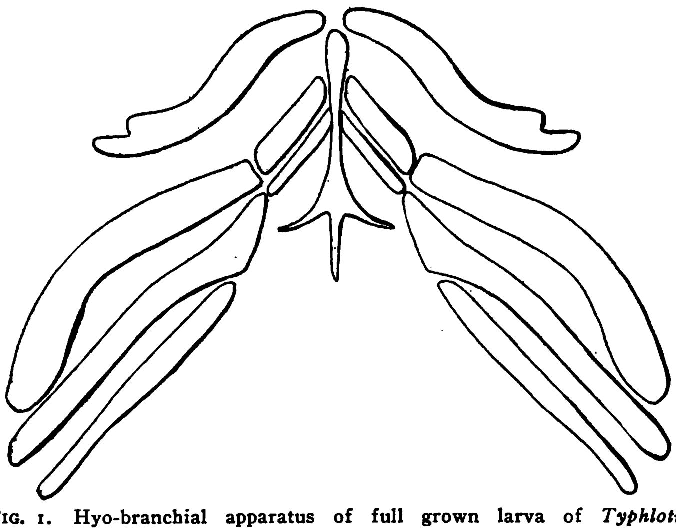

FIG. 1. Hyo-branchial apparatus of full grown larva of *Typhlotriton spelæus* from above, showing three branchial bars and a three-pointed "Copulastiel." × 6.

as large as the adult, only three branchial arches are found, Fig. 1, instead of four which are found in the larvæ of other members of the family Desmognathidæ, Fig. 2.

In the adult *Typhlotriton*, the general character of the hyobranchial apparatus is much like the type found commonly in the

[1] Stejneger, Leonhard, "Preliminary Description of a New Genus and Species of Blind Cave Salamander from North America, *Proc. U. S. Nat. Museum*, Vol. XV., 1892.

family Plethodontidæ, especially in the character of the very long first cerato-branchial, Fig. 3.

By a comparison of the hyo-branchial apparatus of larval *Typhlotriton* with the same parts in the larvæ of the Plethodontidæ, a striking resemblance may be noticed, especially in the fact that in *Typhlotriton* as in *Spelerpes* for instance, Fig. 4, there are only three branchial bars, while the general proportions of all the parts are about the same, as the figures show.

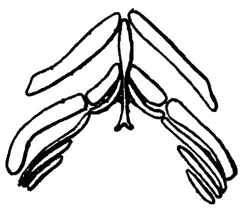

FIG. 2. Hyo-branchial apparatus of nearly full grown larva of *Desmognathus fusca* from above, showing four branchial bars. × 6.

If the hyoid apparatus of *Typhlotriton* larva be compared with that of *Typhlomolge,* another cave form, but one that has external gills, a very striking resemblance is found between the two, Fig. 5. Emerson[1] who describes the hyo-branchial apparatus of this form, suggests that it shows in many ways a marked resemblance to a *Spelerpes* larva and that it differs widely from the members of the family Proteidæ in which it has been placed.

May not this then be a larva, possibly a permanent larva as suggested by Kingsbury[2] for *Necturus?* At any rate judging from the hyoid apparatus alone there seems to be a rather close relationship between the two forms *Typhlomolge* and *Typhlotriton*.

In comparing the hyoid apparatus of *Typhlotriton* with that of larval *Spelerpes,* it may be noted that in all essential respects the two structures are alike. There is a slight difference in the proportions of parts, and the tip of the " Copulastiel " of Gaup, has three parts in *Typhlotriton* while it only has one in *Spelerpes*. The similar one of *Typhlomolge* we find divided into two.

[1] Emerson, 2d, Ellen T., "General Anatomy of *Typhlomolge rathbuni,*" *Proc. Bost. Soc. Nat. Hist.*, Vol. 32, No. 3.

[2] Kingsbury, B. F., "The Rank of *Necturus* among Tailed Bacteria," BIOL. BULL., Vol. VIII., 1905.

A summary of the points in which *Typhlomolge, Typhlotriton* and *Spelerpes* agree would be somewhat as follows:

1. All have three branchial bars in the larval form. The so-called adult, but possible larva *Typhlomolge,* has three.

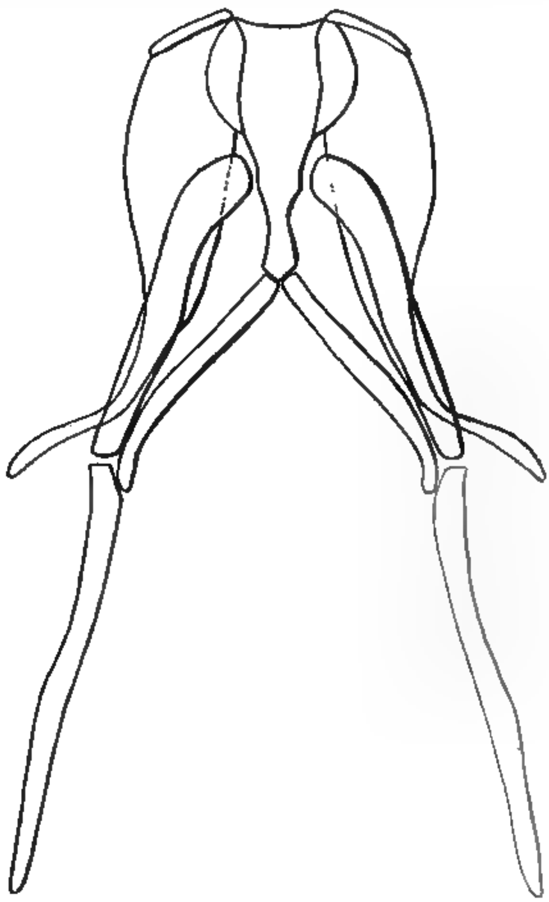

Fig. 3. Hyo-branchial apparatus of adult *Typhlotriton* from below, showing the long projecting 1st cerato-branchial. × 6.

2. The proportions and general position of the parts of the hyo-branchial apparatus are much the same in all.

3. In the adult forms of *Typhlotriton* and *Spelerpes,* the first cerato-branchial is very long.

4. The larvæ of *Typhlotriton* and *Spelerpes* grow to some size before transforming.

5. All forms live away from the light much or all of the time, two have lost the use of their eyes and numbers of the genus *Spelerpes* live in caves to some degree.

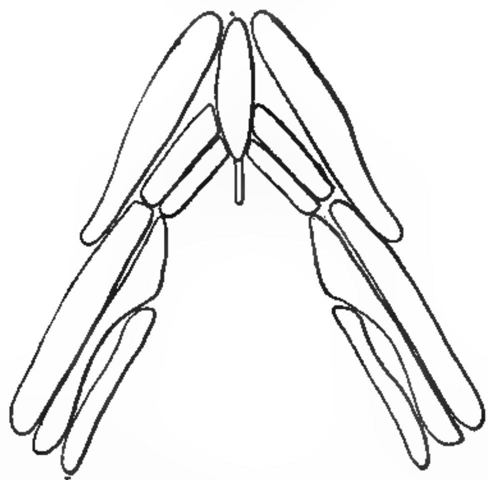

Fig. 4. Hyo-branchial apparatus of full-grown larvæ of *Spelerpes bilineatus* from below, showing the single "Copulastiel." × 6.

Judging from these similarities may not a series of forms be named in which all the members are closely related to each other, and which shows the different degrees of adaptation of one distinct line of Urodela?

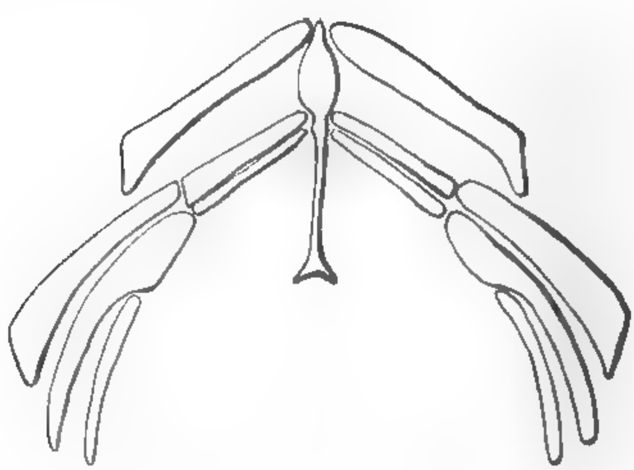

Fig. 5. Hyo-branchial apparatus of *Typhlomolge rathbuni* from above, after Emerson. × 6.

1. *Spelerpes bilineatus* which is not found in caves to any degree.

2. *Spelerpes longicauda* resembling the first form, but often called a cave salamander, although it may be found out from caves now and then.

3. *Spelerpes manculicaudus.* More properly a cave form and closely resembles the next form in many ways on the one hand, as well as *longicauda* on the other, but has well developed eyes.

4. *Typhlotriton,* found in caves. Has lost the use of its eyes and is truly a cave form.

5. *Typhlomolge rathbuni* which is found in deeper caves and seems to be a permanent larva or the larva of an adult closely related to *Typhlotriton* and *Spelerpes.*

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EXTRAIT

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Le développement du chondrocrâne d'Alytes obstetricans avant la métamorphose

PAR LE

Dr W. H. VAN SETERS (La Haye)

(Institut de Zoologie, Université de Leiden)

(Planches VIII et IX et 12 figures dans le texte)

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1922

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PAR LE

Dr W. H. VAN SETERS (La Haye)

(Institut de Zoologie, Université de Leiden)

(Planches VIII et IX et 12 figures dans le texte)

I. — INTRODUCTION

L'Embryologie comparative du chondrocrâne des représentants d'une certaine classe de Vertébrés prendra plus d'importance à mesure que les recherches pourront s'étendre sur les espèces les plus différentes.

Pourtant on peut constater souvent qu'on se borne — et c'est très explicable — à une espèce qui, étant très commune dans une certaine région, donne toujours les stades nécessaires et désirés en abondance. Mais l'inconvénient de cette manière d'agir est que souvent les divers savants examinent, sans le vouloir, les mêmes spécimens.

Les investigations concernant le chondrocrâne des Anoures nous donnent un bel exemple de ce cas.

Dans la littérature on trouve plusieures publications sur *Rana*, particulièrement sur *Rana fusca*. Le développement du chondrocrâne de cette espèce est devenu de plus en plus clair par les œuvres de PARKER (1871), STÖHR (1882), GAUPP (1893) et PEETERS (1910). Les recherches de ces auteurs se sont complétées fort bien. STÖHR examina les stades les plus jeunes dès la première formation prochondrale jusqu'au commencement de la chondrification ; PARKER et GAUPP

ont étudié le développement jusqu'à la métamorphose et pendant celle-ci. Mais malgré le travail soigné et détaillé de ce dernier auteur, il restait nombre de questions que PEETERS put résoudre pour la plupart, en appliquant la nouvelle méthode des préparations totales du chondrocrâne selon VAN WIJHE.

Les autres recherches sur le chondrocrâne de *Rana* et de quelques autres Anoures sont en grande partie de date ancienne, peu nombreuses et incomplètes.

Une étude approfondie du développement d'un chondrocrâne d'Anoures a donc certainement sa raison d'être.

Deux causes ont contribué à me faire choisir une espèce déterminée. Je la voulais plus primitive que *Rana* et assez abondante pour me donner un nombre suffisant de stades.

Alytes obstetricaus répondait à ces deux conditions. Jusqu'à présent cette espèce est assez mal connue.

Le travail de C. VOGT (1842) n'étant pas à ma disposition, j'ignore s'il traite de la question.

RIDEWOOD et KALLIUS ont décrit le développement du squelette hyobranchial. PEETERS (1910) disposa de quelques larves de 25, 43, 50, 53 mm., qu'il put examiner en séries et en préparations totales. Les résultats de cet auteur, qui exprima le désir d'examiner des stades plus jeunes afin de mieux comprendre certaines différences entre *Alytes* et *Rana*, ont été le point de départ de l'étude qui va suivre.

Mes recherches s'étendent depuis la première formation cartilagineuse du chondrocrâne jusqu'à un stade de développement (série 19) assez rapproché de la métamorphose.

Afin de donner une idée plus complète du développement j'ai choisi *deux* de mes séries (stades I et que II), je décrirai séparément, mais en insistant cependant sur les stades antérieurs et intermédiaires.

Le stade I (larve de 7 mm.) est le premier stade qui, grâce à une chondrification suffisante, pouvait être modelé selon la méthode de BORN. On peut le comparer aux jeunes stades de *Rana*, figurés par STÖHR (1882, Taf. III, fig. 18),

Gaupp (1893. Taf. XIII, fig. 1) et Peeters (1910, pl. I, fig. 4).

Le stade II est une larve de 53 mm. (longueur de la queue 31 mm., des pattes postérieures 3 mm., membres antérieurs pas encore libres). Quoiqu'il y ait des points de comparaison avec le deuxième stade de Gaupp (*Rana fusca*, larve de 29 mm.), la longueur suggère déjà la remarque que le développement est plus avancé. Il faut le placer entre les deuxième et troisième stades (*Rana*) de Gaupp.

Pour distinguer les parties du crâne, j'ai suivi la méthode de Gaupp (1893) ; pour cette raison, les suprarostralia sont traités en même temps que les trabécules. La description du développement du palatocarré, du cartilage de Meckel et des infrarostralia, est placée après celle du neurocrâne.

Le développement du squelette hyobranchial, qui est bien connu par les recherches de Ridewood (1898), Kallius (1901) et Peeters (1910) ne nous occupera pas.

Pour comparer j'ai examiné aussi quelques larves de *Pipa americana* et de *Xenopus*, pour lesquelles je remercie particulièrement MM. les Professeurs M. Weber et W. Leche, M. le Docteur H. W. de Graaf et M. Reyne, entomologue à Paramaribo.

La littérature et les considérations générales seront exposées après la description de chaque partie du chondrocrâne.

II. — MATÉRIEL ET TECHNIQUE

Le matériel d'*Alytes*, mis à ma disposition, était conservé dans l'alcool à 96 % ; les stades plus jeunes étaient fixés dans la liqueur de Flemming et dans l'acide picro-sulfurique ; les stades plus avancés à partir de 7 ½ mm. dans ce dernier fixateur et dans la liqueur de Zencker.

Les stades jeunes jusqu'à 7 ½ mm. furent colorés par l'hématoxyline d'Ehrlich et l'éosine, ce qui donna de bons résultats et fit ressortir les ébauches du cartilage. Pour les

stades ultérieurs j'ai appliqué plusieurs méthodes de coloration. A ma grande surprise, j'ai observé que le bleu Victoria, dont je n'espérais rien après fixation au ZENCKER, colorait fortement le cartilage sur les coupes de stades pas trop jeunes.

Le contraste était accentué par décoloration du tissu environnant dans l'alcool à 70 %. Le procédé employé fut le suivant. Les coupes colorées au carmin boracique furent traitées sur porte-objet pendant cinq minutes dans une solution de bleu Victoria à 2 % dans l'alcool à 64 %, puis lavées à l'alcool à 70 % ; ensuite successivement aux alcools à 90 % et à 96 % et colorées pendant un moment dans une solution d'éosine dans l'alcool à 96 %. Le résultat est surprenant : le cartilage est d'un bleu clair, les noyaux d'un rouge foncé et le tissu musculaire, etc. d'un rose pâle. On ne peut appliquer cette méthode de coloration qu'aux larves de 14 mm. jusqu'à la métamorphose. Le cartilage des larves trop jeunes ou trop avancées n'absorbe pas bien le bleu Victoria.

Parfois le protoplasme des larves, colorées in toto par du carmin boracique, fut aussi teint avec du bleu de Lyon, dont le mode d'emploi ressemble tout à fait à celui de l'éosine. Il faut signaler ici que cette matière colorante sert en même temps de réactif pour démontrer les fibres élastiques, fait inconnu dans la littérature que j'ai consultée. Ces fibres élastiques prennent une couleur bleue très claire dans le tissu des poumons, des artères et dans le tissu qui remplit la fenêtre ovale pour fixer l'operculum.

De plus, les cloisons intercellulaires du cartilage, réunissant les hyoides et la copule (pars reuniens) et aussi le tissu, reliant les infrarostralia, prirent intensivement le bleu de Lyon.

On trouvera la liste des séries étudiées dans le tableau (page 377) avec leur numéro, le mode de fixation, la coloration et la direction des coupes. L'épaisseur des coupes était toujours 0.01 mm., excepté celle des séries 19, 20 et 22 (0.015 mm.).

TABLEAU

SÉRIE	Dimensions en mm.				Fixation	Teinture	Direction de coupe	Rem.
	L. tot.	L. d.l.q	L. p. p.	L. p. a.				
1	4 1/2	—	—	—	Fl.	H.E.-E.	Sag.	a
2	4 1/2	—	—	—	»	»	Hor.	b
3	5	—	—	—	»	»	»	c
4	5	—	—	—	P. S.	»	»	—
5	6	—	—	—	»	»	»	—
6	6	—	—	—	»	»	»	—
7	6 1/2	—	—	—	»	»	»	—
8	7	—	—	—	»	»	Transv.	—
9	7	—	—	—	»	»	»	d
10	7 1/2	4	—	—	Z.	B.C.-B.V.-B.L.	»	—
11	8 1/2	5	—	—	»	B.Th.-E.	Sag.	—
12	8 1/2	5	—	—	»	B.C.-B.V.-B.L.	Hor.	—
13	9 1/2	5 1/2	—	—	»	H.E.-E.	Transv.	—
14	12 1/2	7 1/2	—	—	»	B.C.-B.V.-E.	»	e
15	16	8 1/2	—	—	»	»	»	—
16	22	12	—	—	»	»	»	—
17	25	13	—	—	»	B.C.-B.Th.-E.	»	—
18	29	16	1 1/2	—	»	B.C.-B.V.-E.	Hor.	—
19	53	31 1/2	3	—	»	B.C.-B.L.	Transv.	f
20	62	37	18	7	»	»	»	g
21	55	31	30	12 1/2	»	B.C.-B.V.-E.	»	h
22	29	—	43	17 1/2	»	B.C.-B.L.	»	i

Abréviations : B.C. Borax-carmin ; B.L. Bleu de Lyon ; B.Th. Bleu Thionine ; B.V. Bleu Victoria ; E. Eosine ; Fl. Liqueur de Flemming ; H.E. Haematoxyline d'Ehrlich ; L. d. l. q. Longueur de la queue ; L. p. a. Longueur des pattes antérieures ; L. p. p. Longueur des pattes postérieures ; L. tot. Longueur totale ; P. S. Acide picrique-sulfurique ; Z. Liqueur de Zencker.

Remarques : *a*) pas de branchies externes ; œil pas pigmenté ; *b*) idem ; pigmenté ; *c*) branchies externes ; *d*) *stade premier* ; modèle en cire ; *e*) branchies externes disparues ; *f*) *stade second* ; *g*) le pied antérieur gauche pas encore libre ; *h*) la queue est en réduction ; *i*) spiracle disparu.

J'ai étudié le développement du chondrocrâne non seulement sur des coupes, mais aussi sur quelques préparations

totales, montées dans du baume de Canada, colorées au bleu méthylène ou au bleu Victoria, selon la méthode de VAN WIJHE et PEETERS. Le résultat de cette méthode dépend en grande partie du mode de fixation. Après fixation dans la liqueur de ZENKER, j'ai observé une coloration anormale, les noyaux et les capsules cartilagineuses fixaient surtout le bleu méthylène et seulement parfois aussi la substance intercellulaire du cartilage. Mais après fixation dans de l'acide picro-sulfurique, j'ai obtenu des chondrocrânes colorés aussi intensivement et régulièrement qu'après la fixation en sublimé-formol, le fixateur recommandé par PEETERS et VAN WIJHE. Avec des larves très jeunes ou en métamorphose, je n'ai pas obtenu de résultats satisfaisants.

Ce sont donc des larves d'une longueur de 9 à 32 mm., que j'ai étudiées en préparations totales, afin de contrôler et de compléter les observations des mes séries.

Je ne commencerai pas l'exposé de mon travail sans avoir exprimé mes sentiments de reconnaissance envers M. le Docteur H. W. DE GRAAF, conservateur de zoologie à Leiden, qui m'a cédé avec grande bienveillance le matériel d'*Alytes obstetricans*, qu'il avait recueilli et bien fixé depuis longtemps.

III. — PREMIER DÉVELOPPEMENT DU CHONDROCRANE JUSQU'A ET Y COMPRIS LE STADE I

A. Planum basale, Arcus occipitalis, Chorda dorsalis

Stade I *(larve de 7 mm., série 9, Pl. VIII, fig. 1 et 2)*

Des deux côtés de la corde dorsale existe une bande de cartilage (cartilage parachordal) qui s'élargit en direction rostrale, puis se transforme en cartilage des trabécules ; en direction caudale, elle se rétrécit, s'éloigne de la corde et forme le tissu prochondral de l'arc occipital qui se recourbe dorso-latéralement et s'appuie sur la capsule auditive.

Le tissu de l'arc occipital n'est que partiellement changé en cartilage, seule la partie qui s'attache à la capsule est cartilagineuse sur une courte distance. Cette partie est pourtant bien différente du cartilage de la capsule auditive. Les nerfs IX et X sont, du côté caudal, entourés du tissu prochondral qui formera plus tard l'arc occipital cartilagineux.

Le cartilage parachordal se transforme latéralement en cartilage ventro-médial de la capsule auditive. Entre les deux on peut indiquer sur toute la longueur une zone de croissance, visible parce que là le cartilage n'est pas ou à peine développé (Pl. VIII, fig. 1 et 2, indiqué par une ligne pointillée).

Le bout de la corde est courbé dorsalement. Au devant de lui les deux plaques parachordales s'unissent dans le plan trabéculaire impair. Le cartilage dorsal et ventral de l'extrémité de la corde se transforme caudalement en un tissu prochondral encore mince, qui ne couvre le bas côté de la corde que sur une petite distance ; le tissu prochondral au-dessus de la corde diminue de plus en plus en épaisseur caudalement et se compose de cellules très plates, qui se transforment latéralement en cartilage parachordal. Celui-ci est formé d'une masse continue sagittale et garde partout la même épaisseur. Donc il est impossible d'y distinguer, par la forme ou autrement, deux ou trois parties.

Développement

1° *Le planum basale* :

Le plan basal cartilagineux apparaît pour la première fois dans des larves de 6 mm. (les séries 5 et 6). Ni à ces stades, ni dans les larves de 6 ½ mm. (série 7) on n'aperçoit d'union cartilagineuse entre le plan basal et la paroi ventrale de la capsule auditive ; ils sont partout séparés par une bande de tissu non cartilagineux. Dans une larve de 7 mm. (série 8) le plan basal cartilagineux a déjà atteint une grande épaisseur, tandis que le tissu procartilagineux de la capsule auditive, qui s'y joint, s'en distingue en ce qu'il est plus mince de moitié.

Dans le tissu prochondral de la capsule auditive, on trouve un centre particulier de chondrification, ventromédial par rapport au sacculus, qui unira le plan basal et la paroi de la capsule auditive. Il est donc rationnel de voir en ce cartilage qui forme la paroi ventro-médiale de la capsule auditive à partir de ce centre, une partie de cette capsule. La chondrification de cette partie ne provient pas du plan basal, mais s'y réunit secondairement. Il est possible même, dans la série 9, d'indiquer une limite entre elles.

Le plan basal se transforme rostralement en les trabécules. Au commencement, le tissu qui se trouve devant le bout de la corde, n'est pas encore cartilagineux (les séries 2, 3, 4 et 5) ; on trouve le plan trabéculaire non apparié pour la première fois sur une larve de 6 mm. (série 6).

Puisque le plan basal d'une larve de 7 mm., comme j'ai dit plus haut, ne montre ni par une différence d'épaisseur, ni par sa structure une composition complexe, il est intéressant d'examiner d'autres stades du développement à cet égard.

Dès maintenant je puis dire qu'on trouve toujours, non seulement dans les stades cartilagineux, mais aussi dans les stades prochondraux (séries 3 et 4) une bande continue de tissu des deux côtés de la corde dorsale.

Dans les séries 3 et 4 les noyaux du mésenchyme sont très serrés là où se formera plus tard le plan parachordal.

Le développement du cartilage commence à côté du bout de la corde et représente ainsi la première formation du plan trabéculaire. Je n'ai pas trouvé de centre cartilagineux particulier, situé entre les capsules auditives et la corde, qui aurait pu être l'ébauche du cartilage mésotique, parce que le plan parachordal de la série 5 s'est déjà transformé tout à fait en cartilage.

Quoique que je n'aie pu examiner par une méthode directe la composition du plan basal, il est pourtant possible de la déterminer avec assez d'exactitude grâce à d'autres données.

La composition du plan basal a des rapports étroits avec

la question du nombre des segments postauditifs qui appartiennent à la tête et la situation de l'arc occipital, par rapport à ces segments.

En supposant, comme on le fait généralement (GAUPP, 1906 ; PEETERS, 1910), qu'il y a *trois* segments postauditifs et que l'arc occipital est situé entre le dernier myotome postauditif et le premier du tronc, on peut s'attendre, selon l'interprétation de PEETERS, à une composition *triple* du plan basal, c'est-à-dire : 1° le plan trabéculaire ; 2° le cartilage « mésotique », formé à la place de la deuxième plaque musculaire postauditive et 3° le plan occipital, occupant la place de la troisième plaque musculaire postauditive (PEETERS, 1910 : *Rana*).

Mais, si au contraire, il était montré que *deux* segments postauditifs prennent part à la formation de la tête et que l'arc occipital se trouve entre la deuxième plaque musculaire céphalique et la première du tronc, il me semble qu'une composition *dimère* serait probable.

En consultant les séries 2, 3, 4, 7, 12 et 18, j'ai pu examiner l'évolution de cette partie de la tête et je la décrirai brièvement. Les résultats sont réunis dans le schéma 1, pl. IX.

Série 2 (Schéma 1*a* ; fig. 5 et 6, pl. IX) :

Les myotomes se trouvent des deux côtés de la corde, à partir de l'endroit où le n. X quitte le cerveau (fig. 5, pl. IX) ; ils sont encore peu développés. Les myoseptes, ganglions, plaques cuticulaires et artères intersegmentaires sont bien distincts.

Devant le premier myotome rostral (R. S. 1) (1) nous voyons les restes d'une plaque musculaire, partiellement développée (K. S. II). L'arrangement des noyaux du mésenchyme affecte là, dans quelques coupes, dans la partie cau-

(1) Pour abréger, dorénavant je désignerai le 1er segment du tronc par R. S. 1 et le deuxième segment du tronc par R. S. 2 ; le premier segment de la tête postauditif par K. S. I et le second par K. S. II. J'emploierai les mêmes abréviations pour indiquer les plaques musculaires, complètement ou partiellement développées qui appartiennent à ces segments.

dale la forme d'une plaque musculaire que l'on peut considérer comme le début de la formation des fibres musculaires. Le premier myosepte sépare cette partie musculaire de celle de R. S. I (fig. 5 et 6, pl. IX).

En dedans de ce premier myosepte on trouve des deux côtés de la corde une artère, qui part de la racine de l'aorte en direction dorsale. Il est impossible de suivre son parcours au-delà, mais dans les stades suivants elle reparaît comme l'artère occipito-vertébrale. Je la signale parce que sa situation par rapport aux plaques musculaires nous donne un point d'orientation dans cette région.

Les rudiments des ganglions, appartenant aux plaques musculaires, sont partout très nets, excepté celui de la première plaque (R. S. I) qui est moins développé que les autres.

Le mésenchyme de la tête en avant des myotomes et de la corde, laquelle s'étend à peu près jusqu'à la moitié des vésicules auditives, n'atteint pas l'infundibulum et ne montre aucun indice d'une chondrification future.

Série 3 (schéma 1*b*; fig. 7 et 8, pl. IX):

Pour la première fois, on peut observer sur le prolongement rostral de la série des myotomes un arrangement particulier des noyaux du mésenchyme. C'est le début du développement du cartilage parachordal.

Ces deux bandes de mésenchyme se recourbent en dehors au bout de la corde et se perdent dans le mésenchyme de la tête. Devant l'extrémité de la corde elles sont unies par une bande transversale de mésenchyme d'une couleur foncée. La couleur de ce tissu, ainsi que celle des bandes parachordales de mésenchyme est due à l'accumulation des noyaux et au grand nombre de grains vitellins.

La forme de la plaque musculaire dans la partie caudale de K. S. II est encore distincte par suite de l'arrangement des noyaux (fig. 7 et 8, pl. IX), mais le rudiment des fibres musculaires y est à peine visible.

Le rudiment du ganglion du segment R. S. 1 est presque totalement disparu, par contre ceux des autres sont nets. L'artère occipito-vertébrale est située un peu caudalement au myosepte compris entre K. S. II et R. S. 1 (fig. 8).

Série 4 (schéma 1*c* ; fig. 9 et 10, pl. IX) :

Au devant des myotomes du tronc se trouve une bande parachordale de tissu qui, par sa couleur foncée et sa structure, se distingue clairement du mésenchyme ambiant et qu'on peut considérer comme du tissu prochondral (fig. 10, pl. IX.)

Les myotomes R. S. 1 et 2 sont situés comme dans les séries précédentes un peu en arrière des vésicules auditives. On peut reconnaître la partie dorsale de K. S. II par l'ordonnance des noyaux du mésenchyme entre les vésicules auditives et R. S. I.

Le premier myotome du tronc (R. S. 1) dont le ganglion est disparu, est atrophié dans sa partie ventro-médiane (fig. 10) ; ventralement les myotomes se rapprochent de la corde ; l'artère occipito-vertébrale, maintenant située à mi-chemin de R. S. 1, s'engage dans la partie mésenchymatique de ce myotome (fig. 10).

La limite craniale de R. S. 1 est rendue visible par la couleur foncée du tissu parachordal situé en avant de ce myotome (fig. 10). Cette bande parachordale se rétrécit vers la corde, s'élargit et passe dans la base du tissu compact en forme d'U, qui entoure le cerveau ventro-latéralement. Ce tissu prochondral est situé aussi devant la corde.

Du côté caudal le tissu parachordal se transforme progressivement en tissu prochondral de l'arc occipital qui se recourbe un peu dorso-latéralement et disparaît bientôt dans le mésenchyme, derrière la vésicule auditive. Le tissu prochondral de l'arc occipital est situé contre le myosepte K. S. II — R. S. 1 (fig. 9).

Série 7 (schéma 1*d*; fig. 11 et 12, pl. IX) :

Le tissu parachordal prochondral est devenu du cartilage

dans toute sa longueur et se prolonge en direction caudale dans l'arc occipital encore procartilagineux ; celui-ci est situé maintenant entre le ganglion n. X. et R. S. 2, parce qu'à cet endroit R. S. 1 est presque atrophié. L'arc occipital se recourbe caudalement au n. X. vers la vésicule auditive et s'appuye contre le tissu prochondral de la capsule auditive. C'est aussi devant l'extrémité de la corde que le cartilage s'est développé (fig. 12). La partie centrale de R. S. 1 est plus réduite que dans la série 4. Ce n'est que latéralement et dorsalement (fig. 12) qu'on trouve encore des fibres musculaires; là elles s'attachent à la paroi future de la capsule auditive (fig. 11).

L'artère occipito-vertébrale est située à peu près en regard du milieu de la partie ventrale de R. S. 1 (fig. 12). Tous les ganglions se sont développés au même degré et commencent par R. S. 2.

Série 12 (schéma 1*e*; fig. 13, pl. IX) :

Maintenant R. S. 2 s'attache directement à la capsule auditive cartilagineuse, parce que les fibres musculaires dorsales de R. S. 1 sont presque complètement disparues. A l'endroit où l'arc occipital s'unit à la capsule auditive, on peut cependant encore trouver quelques restes des fibres musculaires de R. S. 1 (fig. 13) ; il en est de même dans la partie ventrale. Donc R. S. 1 a presque disparu et sa place est occupée en partie par le plan parachordal qui s'est agrandi en direction caudale. A gauche, l'arc occipital est tout à fait cartilagineux, à l'exception d'une petite partie centrale, mais à droite il est encore procartilagineux.

Le ganglion de R. S. 2 est peu développé ; celui de R. S. 3 l'est davantage, quoique pas autant que ceux qui suivent.

L'artère occipito-vertébrale se trouve dans la bande de tissu mésenchymatique entre R. S. 2 et le plan parachordal.

Série 18 (schéma 1*f*; pl. IX et fig. 1) :

Le cartilage parachordal est bien limité caudalement ;

par sa croissance en arrière les arcs occipitaux, devenus cartilagineux, ont pris une position verticale, différente de celle qu'ils avaient dans les stades précédents, où ils faisaient un angle plus ou moins aigu avec le plan horizontal (fig. 1 et 2, pl. VIII).

A ce stade les vertèbres sont cartilagineuses et, en comparant avec les stades précédents, on peut déterminer l'endroit où se trouvent la 1re et la 2e vertèbre par rapport aux myotomes. Selon la fig. 1, et eu égard aux séries précédentes, il est évident que le deuxième arc vertébral (W. 2) se trouve dans le myosepte de R. S. 2 et R. S. 3.

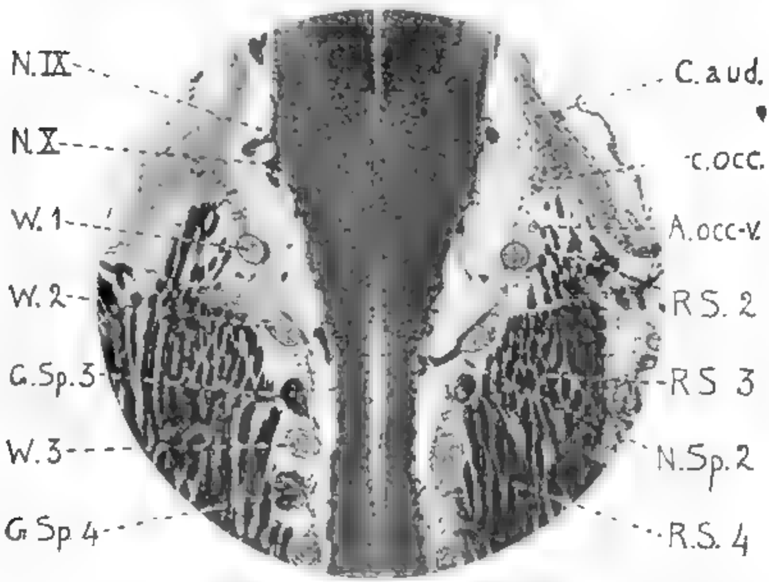

FIG. 1. Coupe horizontale d'une larve de 29 mm. (série 18). *Région occipito-vertebrale.* Gross. 38 × .

A. occ.-v., arteria occipito-vertebralis ; *C. occ.*, crista occipitalis lateralis ; *C. aud.*, capsula auditiva ; *G. sp.* 3 *et* 4, ganglion spinale 3 et 4 ; *N. sp.* 2, nervus spinalis 2 ; *RS* 2, 3 *et* 4, myotomes, appartenant aux segments 2, 3 et 4 du tronc ; *W.* 1, 2 et 3, vertèbres 1, 2 et 3 ; *N. IX et X*, nervus glossopharyngeus et vagus.

Par conséquent, la première vertèbre W. 1 est située entre R. S. 1 et R. S. 2 et l'arc occipital entre K. S. II et R. S. 1. En effet, on peut constater dans la série 4 que le tissu pro-

chondral de l'arc occipital s'appuie contre le myosepte de K. S. II et de R. S. 1.

Faute de séries où j'aurais pu observer le premier développement de la première vertèbre, il me fut impossible de déterminer exactement la place de cette vertèbre, mais d'après le schéma 1*f*, la conjecture susdite est la seule plausible.

Le myotome R. S. 1 est maintenant tout à fait réduit. A la limite du plan parachordal et du corps de la première vertèbre nous trouvons l'artère occipito-vertébrale, qui monte dorsalement entre l'arc occipital et le premier arc vertébral (fig. 1) et se serre étroitement contre la paroi médio-caudale de la capsule auditive. Le point de départ de l'artère est reculé caudalement et se trouve vis-à-vis de R. S. 2.

Tous les nerfs spinaux ont une racine dorsale et une ventrale, excepté le premier, appartenant à R. S. 2 (N. Sp. 2), qui ne possède qu'une racine ventrale (fig. 1).

Résumé. — Pendant le développement, deux segments disparaissent, dont le plus oral (R. S. II) ne montre que dans sa partie caudale la formation passagère de fibres musculaires, peu développées.

Le deuxième segment (R. S. 1) donne un myotome complet mais réduit avec un ganglion peu développé [1].

L'arc occipital se trouve entre K. S. II et R. S. 1 et la première vertèbre entre R. S. 1 et R. S. 2 ; la limite craniovertébrale est située dans le segment R. S. 1. Le myotome R. S. 2 s'attache directement à la capsule auditive ; son ganglion est en réduction et une seule racine spinale se développe. Les autres myotomes ont des racines ventrales et dorsales et des ganglions bien développés.

La position de K. S. II à proximité du ganglion du n. X. dans la série 2 fait supposer que ce nerf X appartient à ce

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[1] Il est possible, selon une observation de la série 3, que quelques fibres musculaires dorsales de R. S. 1 se joignent à celles de R. S. 2 et s'attachent ensemble à la capsule auditive.

segment. Le matériel des stades plus jeunes n'étant pas suffisamment conservé, je ne puis trancher ce point de façon positive. Mais le schéma 1/ montre que cette interprétation est admissible. En effet, R. S. 3 possède une racine ventrale et dorsale, R. S. 2 une racine ventrale (le premier nerf spinal libre) ; un ganglion disparaît qui appartient à R. S. 1 et dont la position est comparable à celle du nerf occipital des Urodèles. K. S. II est donc le segment du N. vague. Le segment du N. IX, que je n'ai pu observer chez Alytes, faute de stades plus jeunes, est situé devant le segment K. S. II (1).

Cela étant admis, il faut conclure que l'arc occipital est situé derrière le deuxième segment postauditif de la tête et qu'il n'a pas la même position que l'arc occipital des Urodèles qui se trouve derrière le troisième segment céphalique (*Necturus* : Miss Platt, 1897 ; *Amblystoma* : Goodrich, 1911).

Par conséquent la tête des Anoures se compose d'un segment de moins que celle des Urodèles. Et le plan basal des Anoures n'est pas identique à celui des Urodèles : celui-ci se compose sans doute de trois parties (le plan trabéculaire, le cartilage mésotique et le plan occipital), celui des Anoures n'a que deux parties (le plan trabéculaire et l'arc occipital).

Nous aurons plus tard l'occasion de comparer notre hypothèse avec celle des auteurs qui ont étudié le développement de la tête et le nombre de segments qui la composent chez les Anoures (cf. les pages 390-394).

2° *L'arc occipital* :

Le début du développement de l'arc occipital s'observe dans une larve de 5 mm. (série 4). Le tissu prochondral est le prolongement du tissu parachordal qui se rétrécit, se recourbe sur les côtés de la corde, puis se dirige un peu dorsalement et disparaît bientôt, parce que les noyaux deviennent

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(1) On l'a trouvé chez Bombinator et Pelobates, comme je le décrirai plus tard.

de plus en plus clairsemés et ne se distinguent plus du mésenchyme environnant. La dernière trace visible de l'arc occipital futur est précisément située devant le premier myotome du tronc (R. S. 1), caudalement au ganglion X et à environ un tiers de la hauteur de la paroi caudale de la capsule auditive (fig. 9, pl. IX). On ne peut pas encore constater d'union avec celle-ci ; nous la verrons pour la première fois dans une larve de 6 mm. (série 8), où l'arc occipital est encore procartilagineux et situé à mi-hauteur de la capsule auditive. Le tissu parachordal s'est transformé dans cette série, comme dans la précédente, en cartilage.

La chondrification de l'arc occipital procède non seulement du côté du plan basal, mais aussi à partir du point de contact de l'arc avec la capsule auditive.

Dans une larve de 9 ½ mm. l'union cartilagineuse du plan basal avec la capsule auditive s'est achevée et ainsi le foramen jugulare est limité par l'arc occipital.

3° *La corde dorsale.*

Quand on examine la position de la corde, à des stades très jeunes, par rapport à l'infundibulum et aux vésicules auditives, on remarque qu'elle s'étend moins loin rostralement qu'on ne pourrait le croire.

Dans une larve de 4 ½ mm. (série 2) le bout de la corde est situé entre les vésicules auditives, mais n'atteint pas la ligne qui réunit leurs centres (fig. 6, pl. IX). l'infundibulum et la fin de la corde restent séparés par un large espace.

J'ai constaté le même fait sur une coupe sagittale d'un stade plus jeune (série 1, larve de 4 ½ mm.).

A des stades plus développés la corde s'étend de plus en plus en direction rostrale. Dans une larve de 5 mm. (série 3) elle atteint le grand diamètre des vésicules auditives ; dans une larve de 5 mm. (série 4) elle le dépasse (fig. 10, pl. IX) et s'approche de plus en plus de l'infundibulum. Le premier cartilage du tissu parachordal est visible dans une larve de 6 mm. (série 5) et on peut y remarquer que le bout de la

corde dépasse la capsule auditive jusqu'à proximité de l'Infundibulum.

Devant le bout de la corde on ne voit pas de cartilage. Ce bout est hémisphérique et il en est de même dans les deux stades suivants (larves de 6 et 6 ½ mm.; séries 6 et 7), où du cartilage existe au devant de l'extrémité de la corde (fig. 12, pl. IX).

Dans une larve de 7 mm. (série 9) le bout de la corde est encore normal. La réduction ne commence à être visible que dans des larves de 8 ½ mm. (séries 11 et 12).

Littérature

1° *Le plan basal* :

Pour Gaupp (1893-1906) chez *Rana fusca* au premier stade, le cartilage situé entre la commissure basicapsulaire antérieure et postérieure au côté ventral du N. VIII et de la partie médiale du sacculus, serait un prolongement latéral du plan basal. Car il dit (1893, p. 373) que, dans une larve de 14 mm.: « Schon jetzt ein Theil des häutigen Labyrinthes seine Stutze von Knorpel erhält, der sich von der Chorda ausgebildet hat, d. h. der den vorgeschobenen Theil der Basalplatte darstellt ». Peeters (1910) professe la même opinion que Gaupp et croit aussi que le cartilage périotique ne prend aucune part à la délimitation de la fenêtre ovale primaire.

L'opinion de Götte (1875) est différente. Il voit chez *Bombinator* que la capsule cartilagineuse de la vésicule auditive s'est formée en même temps que le cartilage parachordal s'est développé. Le bord médial de la capsule s'unit avec la base du crâne en s'agrandissant en direction axiale. Pour cette raison, dit-il, on peut avoir l'impression « als sei wenigstens die horizontale, die Gehörorgane tragende, Platte jener Knorpelkapsel als unmittelbare Fortsetzung der knorpeligen Schädelbasis aus dieser hervorgewachsen ».

En ce qui concerne *Alytes*, je préfère l'opinion de Götte. La petite bande de cartilage, qui apparaît très tôt et que Peeters a décrite, appartient, à mon avis, au cartilage

périotique ; son apparition indépendante au côté latéral des myotomes le prouve.

Puisque le cartilage parachordal d'*Alytes* se développe si tôt et que la partie voisine de la paroi de la capsule auditive ne se chondrifie que plus tard, la limite du plan basal est plus nette ici que chez *Rana.* Le premier stade de GAUPP est déjà trop avancé pour permettre une opinion concernant l'origine des parties diverses du plan basal.

Il vaut donc mieux n'appliquer le terme « plan basal » qu'aux plans cartilagineux qui se trouvent des deux côtés de la corde et non pas au cartilage ventromédial de la fenêtre ovale primaire, qui s'y réunit plus tard.

La composition du plan basal dépend, comme je l'ai dit plus haut, du nombre de segments postauditifs qui prennent part à la formation de la tête et par conséquent il est intéressant d'examiner la littérature concernant ce sujet.

GÖTTE nous donne quelques renseignements au sujet de *Bombinator igneus*, dont voici le résumé.

A son avis, la région céphalique possède quatre segments, dont le premier appartient à la tête antérieure, les trois derniers à la tête postérieure. La vésicule auditive se place entre les deuxième et troisième « äussere Segmente » de la tête, c'est-à-dire entre les rudiments des ganglions VII et IX. J'en conclus que deux segments postauditifs seulement, ceux des N. IX et X, prennent part à la formation de la tête. Il n'y a que le dernier de ces segments qui forme des fibres musculaires dans sa partie caudale (Taf. VII, fig. 122) ; celà est conforme à ce qui se passe chez *Alytes* (schéma 1).

Mais dans sa description (p. 633), GÖTTE, parlant des trois derniers « innere Segmente » de la tête, dit au contraire : « In ihrem Innern ensteht jederseits neben der Wirbelsaite ein Muskelstrang, an den man die Abteilung für das dritte und vierte Segment längere Zeit deutlich, diejenige für das zweite Segment dagegen nur unsicher oder gar nicht erkennt » (Taf. XVI, fig. 303, 304, 314-16). Il faut donc conclure de cette description, que le segment IX pourrait former aussi

des fibres musculaires. Mais l'indication des figures citées ci-dessus (dans lesquelles malheureusement les segments ne sont pas marqués par des lettres) nous fait présumer que Götte s'est trompé en comptant par mégarde le premier segment du tronc comme une partie de la tête ; car il est impossible qu'il existe à des stades aussi avancés des fibres musculaires dans le segment IX. Chiarugi (1891) et Sewertzoff (1895) ont également signalé cette contradiction.

C'est pourquoi je crois que la première interprétation de Götte est juste et que *Bombinator*, comme *Alytes*, ne possède que deux segments postauditifs céphaliques, dont le dernier seul donne des fibres musculaires.

Les résultats de l'étude de *Bufo vulgaris* par Chiarugi (1891) se rapprochent beaucoup de ce qui se passe chez *Alytes*. Chiarugi [1] a exactement vu la formation des nerfs et des ganglions, particulièrement du N. X dans ses rapports avec les myotomes de la tête et du tronc. Il en conclut, que chez *Bufo* il n'y a qu'un segment céphalique, qui produit des fibres musculaires ; celui-ci est dès lors homologue à K. S. II d'*Alytes*.

Le N. X correspond dès son origine à ce segment céphalique; le segment suivant du tronc possède un ganglion, qui disparaît bientôt ; le dernier myotome de la tête et le premier du tronc s'atrophient. La deuxième vertèbre est située entre les deux premiers myotomes définitifs du tronc. On peut appliquer tout ce que je viens de dire à *Alytes*.

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[1] Chiarugi (1891, pp. 229-230) donne les renseignements suivants sur les recherches de Götte sur *Bombinator*. Il les compare avec ses propres résultats chez *Bufo* et dit : « Chez ce dernier (*Bombinator*) il s'en formerait trois (plaques musculaires), une plus antérieure avec des éléments musculaires peu évidents et en arrière deux autres bien constituées; chez le crapaud une seule plaque musculaire est évidentel; a différence de nombre observée ne dépend pas de la formation d'une plaque musculaire en moins, mais de la détermination de la limite, qui divise la série continue des plaques musculaires en plaques, qui correspondent à la tête et en plaques, qui correspondent au tronc. La première des plaques musculaires céphaliques bien constituées du *Bombinator* correspondrait à la plaque musculaire céphalique bien constituée du crapaud, mais la *deuxième céphalique* du *Bombinator* ne serait de fait que la *première du tronc*, aussi bien chez *Bombinator* que chez le crapaud. »

S'il est vrai, comme dit CHIARUGI, que le dernier segment de la tête correspond au N. X, il est permis d'étendre cette conclusion en disant que *Bufo* n'a que deux segments céphaliques postauditifs, c'est-à-dire ceux de N. IX et X.

SEWERTZOFF (1895) a examiné des embryons très jeunes de *Pelobates fuscus*, chez lesquels la position des somites céphaliques par rapport aux ganglions VII, IX et X était clairement visible. Ses résultats concordent avec la première opinion de GÖTTE, c'est-à-dire que les deux derniers segments internes (Kopfhöhlen) correspondent aux ganglions IX et X. Le troisième somite céphalique observé par SEWERTZOFF, celui du N. X (donc le deuxième postauditif) se transforme en un myotome, qu'on peut comparer au myotome de *Bufo*. Les somites des nerfs VII et IX disparaissent sans former des fibres musculaires. Le myotome du N. X (K. S. II d'*Alytes*) s'atrophie, de même que le premier myotome du tronc (R. S. 1 d'*Alytes*). Le myotome de la tête, qui disparaît, est situé devant l'arc occipital.

Selon SEWERTZOFF on trouve donc dans la tête de *Bufo* *trois* somites (GÖTTE put en constater quatre chez *Bombinator*, c'est-à-dire celui du N. V en plus), dont les *deux* derniers doivent être très probablement rapportés par comparaison avec *Bombinator*, à la région postauditive (voir note de SEWERTZOFF, 1895, p. 268).

Les résultats de CHIARUGI, SEWERTZOFF et aussi ceux de GÖTTE (après correction) concordent en grande partie. Aussi peut-on s'étonner de voir que PEETERS (1910) s'en écarte, pour ce qui concerne *Rana fusca* et *esculenta*.

PEETERS a trouvé chez des larves de *Rana fusca* de 8 mm. et de *Rana esculenta* de 6 mm. deux myotomes qui s'étendent entre les capsules auditives, des deux côtés de la corde jusqu'au plan trabéculaire. La limite caudale du deuxième myotome coïncide avec celle de la capsule auditive. Ces deux myotomes sont éphémères. Le premier disparaît chez une larve de 9 ½ mm. (*Rana fusca*), le deuxième est presque entièrement résorbé chez une larve de 11 mm. La place des deux myotomes est occupée par le plan basal. Il semble même que le

deuxième myotome se transforme immédiatement en cartilage. Selon PEETERS un tel mode de développement prouve la trimérie du plan basal : le plan trabéculaire, le cartilage mésotique à la place du 1er myotome et le plan occipital à la place du 2e myotome ou même provenant de celui-ci.

Il me semble que les données de PEETERS ne sont pas tout à fait conformes à la réalité.

J'ai examiné ce point sur quelques séries de coupes horizontales de *Rana fusca*. Dans une larve de 6 ½ mm. je trouvai des myotomes des deux côtés de la corde. Le premier était vis-à-vis du ganglion X, à une grande distance, en direction caudale, de la vésicule auditive et encore plus éloigné du bout de la corde qui s'étend jusqu'à l'infundibulum. Au devant de ces myotomes les noyaux du mésenchyme sont dispersés. Dans une larve de 7 ½ mm. le premier myotome se trouve vis-à-vis du ganglion X, mais son bord rostral dépasse un peu la limite caudale de la vésicule auditive. Les noyaux du mésenchyme devant les myotomes se sont rangés maintenant et se condensent autour du plan trabéculaire prochondral et déjà nettement visible.

Dans une larve de 9 mm. le premier myotome est situé entre les capsules auditives ; son bord caudal correspond à la limite caudale de cette capsule. Le ganglion X est vis-à-vis du myosepte des myotomes 1 et 2. Le plan trabéculaire est cartilagineux. Entre le premier myotome et le plan trabéculaire on voit une bande de tissu, dans laquelle les noyaux du mésenchyme sont très serrés. Dans le plan trabéculaire et dans ce tissu prochondral on peut reconnaître la forme future du plan basal. La présence des ganglions n'a pas pu être constatée exactement pour tous les myotomes ; le premier myotome ne possède probablement pas de ganglion propre.

Quand nous comparons ceci aux observations faites chez *Alytes*, nous constatons un certain accord.

Le premier myotome de *Rana* correspond à R. S. 1 d'*Alytes* ; le mésenchyme devant celui-ci nous fait présumer par son arrangement la présence de K. S. II, dont les fibres musculaires doivent être disparues dans une larve de 6 ½ mm.

Le changement de position du premier myotome par rapport à la vésicule auditive dépend d'un phénomène, observé par SEWERTZOFF (1895) chez *Pelobates* et aussi par moi chez *Alytes*, que l'on nomme « das Einrücken der Myotome in die occipitale Region ».

Le myotome R. S. 1 va disparaître tout comme chez *Alytes*. Je ne comprends pas comment PEETERS peut parler d'une série de myotomes, qui s'étend jusqu'au plan trabéculaire chez des larves de 8 mm. de *Rana fusca*. Déjà à un stade plus jeune (6 mm.), lorsque le plan trabéculaire n'est pas encore formé, il existe un grand espace entre la capsule auditive et les myotomes. Cet espace se réduit par l'invasion des myotomes dans la région occipitale, mais ne disparaît jamais (larve de 9 ½ mm.).

De même je ne puis pas comprendre, comment le myotome correspondant à R. S. 1 d'*Alytes* (probablement le deuxième de PEETERS) se chondrifierait. Quoique les séries nécessaires m'aient manqué, il me semble que ce myotome s'atrophie comme chez *Alytes* et *Bufo* et que sa place est occupée par le plan basal, croissant en direction caudale, ou par un plan occipital se développant plus indépendamment.

PEETERS ne donne pas de renseignements sur la position de l'arc occipital par rapport aux myotomes ; une étude plus approfondie de ces points est donc nécessaire.

En me basant sur les résultats fournis par *Bombinator*, *Bufo*, *Pelobates* et *Alytes*, je crois pouvoir soutenir l'opinion, que chez les *Anoures deux somites postauditifs* seulement prennent part à la formation de la tête.

Considérons maintenant à cet égard les *Urodèles*. Ici, nous trouvons, contrairement aux Anoures, trois somites postauditifs entre la capsule auditive et l'arc occipital. Si nous laissons de côté l'opinoin de SEWERTZOFF (1895) sur *Siredon*, parce que l'investigation ultérieure de GOODRICH (1911) est plus plausible, nous pouvons dire que cela est aujourd'hui généralement accepté (DELSMAN 1917).

MISS PLATT (1897) examina *Necturus*, GOODRICH (1911)

Amblystoma et tous deux trouvèrent trois somites postauditifs, c'est-à-dire ceux des N. IX, X et X_1 ou nerf occipital.

Chez *Necturus* le premier somite postauditif disparaît et le deuxième forme des fibres musculaires, dont les ventrales s'atrophient bientôt ; les fibres dorsales persistent et s'unissent aux fibres musculaires du myotome suivant. L'arc praeoccipital est situé dans le septum entre le deuxième et le troisième myotomes postauditifs, tandis que l'arc occipital se trouve entre le troisième et le quatrième (¹). Le ganglion du N. X correspond au deuxième segment postauditif, celui du N. X_1 au troisième et les deux racines ventrales qui forment le N. hypoglosse correspondent aux 4e et 5e.

L'étude de GOODRICH (1911) sur *Amblystoma* conduit au même résultat ou n'en diffère que dans quelques petits détails. Dans certains stades il trouve une racine ventrale dans le troisième segment postauditif et de plus dans le cinquième une racine dorsale. La partie dorsale des deuxième et troisième myotomes postauditifs persiste. Tout comme chez *Necturus* l'arc praeoccipital se forme entre le deuxième et le troisième segment postauditif ; l'arc occipital entre le troisième et le quatrième; entre l'arc occipital et la première vertèbre, la racine ventrale d'un nerf se montre et forme le N. hypoglosse en se joignant à la racine ventrale suivante, qui prend son origine entre la première et la deuxième vertèbre.

PEETERS (1910) observa aussi chez *Triton* deux myotomes postauditifs, qui se développent aux dépens des deuxième et troisième somites postauditifs ; le premier myotome disparaît. Un peu au-devant du deuxième myotome un centre cartilagineux isolé devient visible ; il est situé du côté médial de la capsule auditive et bientôt il atteint la corde dorsale. L'arc occipital se développe devant le septum entre les

(¹) PEETERS (1910) nie la présence d'un arc praeoccipital cartilagineux chez *Necturus*, parce qu'il n'a pas pu l'observer dans ses préparations.

deuxième et troisième myotomes postauditifs (1), qui s'accroît en bas le long de la corde, s'agrandit et devient le plan occipital. Ici nous voyons clairement le plan basal se former de trois parties différentes : le plan trabéculaire, le centre cartilagineux (la « cartilago mediotica ») et le plan occipital.

Réunissons les données acquises chez les Urodèles en un schéma (schéma 2, pl. IX) et comparons ce schéma avec les résultats acquis chez *Alytes* pris comme exemple d'un Anoure (2).

Le segment 1 (N. IX) disparaît chez tous deux à un stade très jeune ; le segment 2 (N. X) forme chez les Urodèles, du côté dorsal et ventral, des fibres musculaires, dont les dorsales persistent ; chez les Anoures le développement de ces fibres est passager; le segment 3 (N. X_1; K. S. III des Urodèles = R. S. 1 des Anoures) produit chez les Urodèles des fibres musculaires qui restent intactes (*Necturus*) ou dont il ne persiste que la partie dorsale (*Amblystoma*) ; chez les Anoures, ce myotome disparaît aussi dans le cours du développement; les autres segments sont les mêmes chez tous deux.

Le segment 1 correspond au N. IX, le segment 2 au N. X, le segment 3 au N. X_1, qui chez les Urodèles s'unit au N. X (*Necturus*) ou disparaît pendant le développement (*Amblystoma*) et s'atrophie chez les Anoures ; le segment 4 dans les deux groupes possède une racine ventrale du N. hypoglosse ; le segment 5 ne montre que chez *Necturus* une racine ventrale, mais chez *Amblystoma* il possède une racine dorsale et une ventrale qui forme avec la racine ventrale précédente le N. hypoglosse. Chez *Alytes* nous trouvons en ce point une racine dorsale et une ventrale. Il m'a été impossible de constater si cette racine participe aussi au N. hypoglosse (il est certain qu'il n'en est pas ainsi chez *Bombinator*).

Entre les segments 2 et 3 on trouve chez les Urodèles l'arc praeoccipital, chez les Anoures l'arc occipital ; entre les seg-

(1) C'est donc le troisième et quatrième somite postauditif.

(2) Ce schéma nous montre la situation définitive chez les Urodèles et les Anoures ; on trouve les changements qui se produisent pendant le cours du développement dans la description.

ments 3 et 4 chez les Urodèles l'arc occipital, chez les Anoures la première vertèbre.

Il est donc très probable que *l'arc praeoccipital des Urodèles est homologue à l'arc occipital des Anoures* ; *l'atlas des Urodèles n'a donc pas la même situation que celui des Anoures.*

En remarquant que la tête des Anoures contient un segment de moins que la tête des Urodèles, nous pouvons nous attendre à y voir un plan basal, formé de *deux* composants tout au plus et non pas de trois.

Jusqu'à présent je n'ai pas parlé des Gymnophiones. Grâce aux investigations de MARCUS (1906) sur *Hypogeophis*, on a maintenant quelques données sur cette question. Mais ces données devraient être contrôlées ; c'est pourquoi je ne les ai pas utilisées dans le schéma 2.

MARCUS trouve dans la tête quatre somites postauditifs (1) et deux somites praeauditifs (voir MARCUS, les reconstructions 1-8, Taf. 25).

Comme MARCUS ne donne point de renseignements précis sur la situation des nerfs *w* et *x* (nomenclature de FÜRBRINGER), je n'avancerai rien à la légère sur les rapports entre les nerfs et les somites. Néanmoins il est fort intéressant d'observer que nous trouvons dans la tête des Gymnophiones un segment postauditif de plus que chez les Urodèles. Donc il est plus plausible de trouver chez les Anoures un segment de moins que chez les Urodèles et nous ne pouvons pas dire à priori comme GAUPP (1906, p. 721) : « dass die Ausdehnung des Anuren-craniums in kaudaler Richtung die gleiche ist, wie die des Urodelen-craniums, ist fraglos » (2).

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(1) DELSMAN (1917) en doute et attribue aux Gymnophiones aussi *trois* segments postauditifs.

(2) Les considérations suivantes peuvent appuyer la conjecture que la tête des Anoures contient un segment de moins que celle des Urodèles :

1° Il est remarquable que le caractère vertébral de l'arc occipital des Anoures est moins distinct que celui des Urodèles. Ceux-là nous montrent une bande de tissu qui monte en direction dorsale entre les capsules auditives, s'y attache et ensuite se chondrifie ; ceux-ci montrent un arc occipital et sa base, qui sont clairement limités et détachés, en arrière de la capsule auditive (c. f. p. e. PEETERS, 1910, pl. 1, fig. 3,

Voyons maintenant les connaissances *positives* que l'on possède sur la composition du plan basal chez les Anoures et à quel point ceux-ci étaient la supposition de *deux* composants.

Le terme « cartilage mésotique » est employé pour la première fois par STÖHR (1882) chez les Anoures. On voit, selon STÖHR, chez *Rana temporaria*, derrière l'ébauche paire du plan trabéculaire une bande de tissu qui se transforme de suite, sans stade procartilagineux, en cartilage. Ce cartilage diffère d'abord de celui du plan trabéculaire, parce que ses éléments sont plus petits et entourés de plus de substance intercellulaire. Ces deux ébauches cartilagineuses touchent des deux côtés la corde ; le cartilage « mésotique » s'unit latéralement à la mince rallonge du plan trabéculaire.

En ce point les deux bandes sont très étroites. STÖHR n'a jamais vu que ces deux plans cartilagineux fussent séparés l'un de l'autre ; pourtant il admet une origine indépendante du cartilage mésotique, en notant aussi que la plus grande formation du cartilage siège en un endroit situé derrière la région de transition de ces deux plans.

Derrière le cartilage mésotique l'arc occipital se forme, selon STÖHR, indépendamment et s'unit secondairement au cartilage mésotique.

Nous pouvons donc reconnaître à la base du crâne trois par-

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pour *Necturus* et fig. 2 pour *Triton* et mon modèle d'*Alytes*, pl. 1, fig. 1 et 2).

2° On n'a jamais observé l'arc praeoccipital chez les Anoures.

3° La première vertèbre des Anoures n'est jamais perforée comme chez les Urodèles. (La première vertèbre de *Pipa americana* est une vertèbre double (RIDEWOOD, 1897)). Chez les Urodèles, dans le stade larvaire, le premier nerf spinal ventral se trouve complètement dégagé, auprès de l'articulation du crâne et de l'atlas, mais dans le cours du développement il est entouré à cet endroit dangereux par le cartilage de l'atlas (DE GAAY FORTMAN, 1918), qui s'ossifiera plus tard et deviendra la cause de la perforation de cette vertèbre. Le premier nerf spinal des Anoures disparaît et ne peut donc pas causer une perforation.

4° On trouve chez plusieurs Anoures une continuité épicordale de la base du crâne et de l'atlas, laquelle est passagère (c. f. chez GÖTTE, 1875, fig. 164, 165, 166) ; je l'ai observé moi-même chez *Pipa americana* (RIDEWOOD, 1897, de même). Ceci pourrait indiquer une connexité antérieure du crâne et de la première vertèbre.

ties, dont les deux premières ne montrent aucune séparation à aucun stade, soit *a* le plan trabéculaire, *b* le cartilage mésotique et *c* l'arc occipital. Le dernier se développe, quand *a* et *b* sont déjà tout à fait cartilagineux.

Il faut observer que Stöhr en traitant des Anoures ne parle pas, comme il le fait (1880) à propos des Urodèles, de la formation indépendante de la base de l'arc occipital. Selon lui, chez les Urodèles, le plan trabéculaire se forme d'abord, ensuite l'arc occipital, dont les « Basaltheile » s'allongent en direction orale et finissent par s'unir, tandis que le cartilage mésotique (qu'il nomme encore cartilage périphérique) se développe à côté, sans toucher la corde.

La comparaison des deux groupes n'est pas si simple que Stöhr (1882) le suggère, lorsqu'il dit que les trois composants apparaissent en ordre divers, c'est-à-dire chez les Anoures *a, b, c,* chez les Urodèles *a, c, b* (c'est pourquoi *b* apparaît isolé ici).

Gaupp (1893) et Peeters (1910) ont déjà remarqué que la région occipitale est difficile à interpréter : en effet, Stöhr (comme je l'ai dit), n'a parlé de l'*arc* occipital que chez *Rana* et non pas du *plan* occipital. Et dès lors on peut poser cette question : où faut-il chercher chez les Anoures l'homologon du plan occipital des Urodèles ?

L'alternative est formulée par Gaupp (1893, p. 357) en ces termes :

« 1° dieser Abschnitt ist schon in der völlig ausgebildeten Basalplatte, wie sie bei Larven von 15 m. M. besteht, vorhanden ; diese repräsentiere also bereits : Balkenplatte + mesotischen Knorpel + « Occipitalplatte », oder

2° die Basalplatte dieses Stadiums sei nur : Balkenplatte + mesotischen Knorpel, und die Anlagen der erst später verknorpelnden Occipitalbogen hätten mit ihren basalen Theilen die Chorda gar nicht erst erreicht, oder seien doch schon frühzeitig von der Chorda abgedrängt und daher nur mit den seitlichen Theilen der Basalplatte (des mesotischen Knorpels) verbunden ».

Dans le premier cas, il faut supposer que la base de l'arc occipital se chondrifierait avant l'arc lui-même, mais cela serait le contraire de la disposition des Urodèles et du mode général de formation des vertèbres, où l'arc et la base apparaissent en même temps.

C'est pourquoi GAUPP préfère la deuxième éventualité et suggère que chez les Anoures le rudiment de l'arc occipital, rejeté de côté par le déplacement en direction orale du rudiment de la première vertèbre, est forcé de se fusionner aux parties plus latérales du plan basal.

Il me semble que ces deux conjectures ne sont pas tout à fait conformes à la réalité.

Quant au premier cas, GAUPP lui-même nous dit que la base de la première vertèbre se chondrifie *avant* l'arc occipital et il est admissible qu'il se soit produit des changements dans l'ordre chronologique du développement sous l'influence de la capsule auditive.

La deuxième conjecture est à mon avis une interprétation spécieuse parce qu'elle veut maintenir à priori la trimérie du plan basal, qu'on ne peut pas constater dans l'ontogénie.

Ni GAUPP, ni STÖHR ne peuvent délimiter exactement le plan occipital, quoique GAUPP (1893) ait observé dans le plan basal des différences d'épaisseur : la partie centrale du plan est plus mince et se trouve plus ventro-latéralement par rapport à la corde que les deux autres parties. Mais on pourrait admettre avec autant de raison, que cela serait la région de transition entre les *deux* parties du plan basal. C'est ce que STÖHR admet en effet; et il le montre par ses dessins.

Les renseignements de STÖHR et de GAUPP ne confirment pas la conclusion que le plan basal des Anoures serait constitué comme chez les Urodèles, de trois composants.

PEETERS (1910) aussi admet une composition tripartite du plan basal à cause de la disposition des myotomes.

Il trouve deux myotomes, dont la place est occupée par du cartilage. Le premier produit le cartilage mésotique, le deuxième le plan occipital. Celui-ci, qui pénètre comme un

coin entre la corde et le cartilage mésotique, se délimite bien du cartilage, situé devant lui. Une bande de tissu non cartilagineux s'élève du plan occipital jusqu'à la capsule auditive.

Il n'est pas étonnant que PEETERS ait vu une formation indépendante de la base de l'arc occipital, car, en théorie, on peut s'y attendre. Mais un point faible est qu'il dit que le premier myotome se chondrifierait. Puisque PEETERS n'indique pas la situation des myotomes par des figures et n'examine pas non plus leur développement, il est fort difficile de se faire une idée nette de la valeur de son interprétation.

On peut cependant l'exprimer de la manière suivante : PEETERS a observé ce que j'ai nommé chez *Alytes* K. S. II et R. S. 1 ; il est impossible qu'il ait vu K. S. I sous forme de myotome, car celui-ci ne donne jamais de fibres musculaires ; K. S. II, en tant que myotome existe très probablement si l'on s'en rapporte aux dispositions réalisées chez *Bufo*. K. S. II est remplacé, comme chez *Alytes*, par du cartilage. Quand on n'examine pas exactement la position de l'arc occipital par rapport à K. S. II et R. S. I, sur laquelle PEETERS ne donne pas de renseignements, on peut croire que, par la réduction de R. S. 1 et l'agrandissement en direction caudale du plan basal, R. S. 1 lui-même aussi s'est chondrifié et que l'arc occipital est situé entre R. S. 1 et R. S. 2.

Cette supposition devient plus vraisemblable quand on compare à cet égard *Rana fusca* et *Alytes obstetricans*.

L'arc occipital d'*Alytes* est bien marqué dès le début du développement et déjà visible chez une larve de 5 mm. (série 4, fig. 9, pl. IX).

Chez une larve de 7 mm. (modèle) j'ai déjà pu modeler l'arc occipital, pas encore cartilagineux, mais pourtant bien distinct. Chez une larve de 9 ½ mm. (série 13) l'arc occipital est déjà tout à fait cartilagineux ; à ce stade le plan internasal n'existe pas encore.

Chez une larve de *Rana fusca* de 12 mm. avec un plan internasal bien développé, j'ai trouvé le myotome R. S. 1 en réduction, formant du pigment, et l'arc occipital va-

guement marqué ; chez une larve de 14 mm. celui-ci n'est pas encore cartilagineux.

Il est naturellement difficile de comparer les modes de développement, indiqués plus haut, en se basant sur les dimensions des larves ; mais ce qui est certain, c'est que la chondrification dans la région occipitale d'*Alytes* a lieu plus vite et plus tôt que chez *Rana* (comparez par exemple le modèle du crâne d'*Alytes* de 7 mm., où la capsule auditive est aussi développée que celle du modèle du crâne de *Rana* 14 m. M. de GAUPP, tandis que chez celui-ci le plan internasal est déjà formé).

Grâce au fait que la partie caudale du crâne d'*Alytes* se chondrifie si tôt, on peut apercevoir de bonne heure le rudiment de l'arc occipital et l'on peut mieux déterminer ses rapports avec les myotomes que chez *Rana*. Quand on voit chez *Rana* l'arc occipital procartilagineux, R. S. 1 est déjà si réduit, qu'il semble que l'arc occipital appartienne à la partie caudale de ce myotome, tandis qu'il correspond en réalité au K. S. II précédent.

Quant à *Rana*, il est fort désirable qu'on en fasse une nouvelle étude en recherchant attentivement la disposition, puis l'atrophie des myotomes de la région occipito-vertébrale et des ganglions correspondants.

Après ce que je viens de dire, il est évident qu'il est impossible de définir chez les Anoures le terme « cartilage mésotique ». En admettant au contraire que ce cartilage manque chez les Anoures et que le plan basal n'ait ici que deux composants : le plan trabéculaire et le plan occipital, on peut donner une interprétation plus plausible des données de STÖHR et de PEETERS. Les deux suppositions de GAUPP ne me semblent pas justes. Le cartilage, nommé par lui et les autres « cartilage mésotique », n'est en réalité pour moi que le plan occipital.

La composition dimère du plan basal des Anoures, déjà indiquée par l'absence du troisième segment postauditif de la tête, devient aussi plus problable par les résultats de l'étude de l'ontogénie de ce cartilage.

Chez les *Urodèles* on a clairement observé le développe-

ment du plan basal par la concrescence de*t rois* parties.

Déjà en 1880 Stöhr nous apprend que les « occipitalia » de *Triton* et de *Siredon* se montrent séparés l'un de l'autre. Ceux-ci se forment après le développement du plan trabéculaire, mais avant la formation de la capsule auditive (fig. 12, 13, taf. XXIX). Plus tard, des parties latérales, que Stöhr nomme « cartilage périphérique » se joignent à ces deux pièces séparées et accouplées. Il n'a pourtant pas pu voir dans un certain stade, si ce cartilage périphérique se forme indépendamment.

Peeters (1910) put observer le développement isolé de ce cartilage, car il vit un centre cartilagineux, situé du côté médial de la capsule auditive à même distance du bord rostral de l'arc occipital que du plan trabéculaire et devant le myosepte des myotomes 1 et 2. Bientôt il atteint la corde. Voilà pourquoi Peeters croit avoir démontré la composition trimère du plan basal des Urodèles.

Quelle est la signification de ce centre cartilagineux isolé? Selon Peeters il ne se rapporte pas au cartilage de la capsule auditive; donc il ne lui donne pas le nom de cartilage périphérique ou mésotique, mais de « cartilago mediotica ». Et à cause de la situation trop latérale par rapport à la corde, on ne peut le considérer, selon lui, comme l'homologue de la base de l'arc occipital.

Je ne suis pas entièrement d'accord avec cette dernière conclusion. A mon avis, la situation par rapport aux myotomes (dans le schéma 2, devant le myosepte des segments 2 et 3) pourrait indiquer que cette pièce cartilagineuse devrait être considérée comme une partie de la base d'une vertèbre qui précèderait la base de la vertèbre occipitale. Car chez *Necturus* et *Amblystoma* on trouve à la même place, mais plus en direction dorsale, le reste d'un arc vertébral.

Miss Platt a trouvé cet arc praeoccipital chez *Necturus* (1897, p. 448) « in the plane, separating the second postotic somite from the third », comme un « rudimentary neural arch, which is taken into the median wall of the auditory capsule ». Et selon Goodrich (1911, p. 104) un « rudimen-

tary praeoccipital arch, which is taken into the auditory capsule » se développe chez *Amblystoma* entre les deuxième et troisième somites postauditifs.

C'est pourquoi je crois que le «cartilago mediotica» de *Triton* et l'arc praeoccipital d'*Amblystoma* et de *Necturus* sont probablement des restes d'une vertèbre praeoccipitale, développée insuffisamment sous l'influence de la capsule auditive.

Chez *Necturus* et *Amblystoma* une composition trimère du plan basal n'a pas encore été observée, mais elle est théoriquement probable.

La composition du plan basal d'*Ichtyophis* (Gymnophiones) n'est pas déterminée par Peter (1898).

Si nous comparons encore une fois les Anoures avec les Urodèles, en tenant compte de ce que je viens de dire, nous verrons clairement (schéma 2) que l'arc occipital des Anoures correspond à l'arc praeoccipital des Urodèles, ce qui résulte de leur position par rapport aux segments postauditifs. L'arc praeoccipital des Urodèles nous fait supposer un plan praeoccipital comme base vertébrale et comme tel nous pouvons admettre chez eux l'existence du composant central du plan basal, c'est-à-dire le cartilage médiotique.

La composition trimère du plan basal est démontrée chez Triton, parmi les Urodèles, par l'ontogénie, mais pas chez les Anoures ; en théorie on ne peut s'attendre ici qu'à deux composants.

Le plan basal des Urodèles est donc composé du plan trabéculaire, du cartilage médiotique (plan praeoccipital) et du plan occipital ; chez les Anoures on trouve seulement le plan trabéculaire et le plan occipital.

2° *L'arc occipital.*

Gaupp (1893) et Peeters (1910) nous donnent une description de la formation de l'arc occipital chez *Rana fusca*, qu'on peut aussi appliquer à *Alytes*.

Il est curieux que Peeters ait vu le même degré de développement de l'arc occipital chez *Rana fusca* de 11 et 11 ½ mm. que j'ai trouvé moi-même chez des larves d'*Alytes*

de 5 et 6 mm. Ce qui prouve de nouveau le développement rapide de la partie caudale du crâne de cette espèce.

Gaupp et Peeters sont aussi d'accord dans leur description de la concrescence de l'arc occipital cartilagineux avec la « crista occipitalis lateralis » de la capsule auditive. Evidemment le développement de l'arc occipital tire son origine du plan basal et se poursuit en direction dorsale. Il est cartilagineux chez une larve de 21 mm. La première vertèbre commence déjà à se chondrifier dans des larves de 15 mm. A cet égard, *Alytes* est bien différent de *Rana*. Déjà dans des larves de 9 ½ mm. d'*Alytes* l'arc occipital est cartilagineux, tandis que l'atlas ne se chondrifie que dans des larves d'une longueur de 16 à 22 mm.

Le développement de la région occipitale de *Rana* se fait donc à peu près en même temps que celui de l'atlas ; chez *Alytes*, au contraire, l'arc occipital se développe avant la première vertèbre.

Il n'y a pas de crête occipitale latérale dans les jeunes stades d'*Alytes*, mais plus tard elle apparaît dans la même région que chez *Rana*.

3° *La corde dorsale.*

La corde des Anoures s'étend habituellement dans les jeunes stades jusqu'à l'Infundibulum. La disposition chez *Alytes* est donc une exception due à une réduction précoce. Selon Bergfeldt (1897) on trouve chez *Alytes* à un stade (14 myomères), où la corde n'est pas encore vacuolisée, entre le bout de la corde (qui s'étend à peu près jusqu'à l'otocyste) et la base du « mittleren Schädelbalken » (Mittelhirnpolster, Gaupp, 1906), des amas de cellules, qui tirent leur origine de la corde, laquelle s'étendait auparavant jusqu'à cet endroit.

Parmi les Amphibiens je n'ai trouvé dans la littérature qu'un seul cas analogue : c'est *Necturus* (Buchs, 1901). Cet auteur représente sur une coupe sagittale (fig. 19, Taf. XXVII) d'un stade jeune (13 mm.) une disposition analogue de la corde. Les observations d'Eycleshеymer et de Wil-

SON (1910) sur la variabilité de position de l'extrémité de la corde par rapport à l'hypophyse de cette espèce, confirment cette analogie.

Du fait que l'on trouve chez *Alytes* grâce à une réduction très précoce un espace entre l'Infundibulum et le bout de la corde, il se peut que les plans parachordaux s'unissent devant la corde, sans l'influencer d'aucune façon. C'est pourquoi on ne voit pas chez *Alytes*, dans les jeunes stades, les indices d'une réduction de l'extrémité de la corde dorsale, tandis que chez les autres Anoures, le fait qu'elle est revêtue de cartilage dorsalement et ventralement provoque cette réduction.

B. Capsula auditiva

Stade I

Le développement de la vésicule auditive à ce stade répond à la description que GAUPP (1893) a donnée d'une larve de *Rana* de 14 mm. Les trois canaux semi-circulaires sont déjà séparés de la cavité utriculo-sacculaire. Il n'est donc pas surprenant que, par la concordance entre le degré du développement de la vésicule membraneuse et du cartilage qui l'entourera, la capsule auditive elle-même nous montre une grande ressemblance avec le premier modèle de GAUPP (1893 fig. 1, Taf. XIII).

La capsule auditive n'est que partiellement chondrifiée ; sa paroi médiale manque tout à fait, la partie dorso-latérale en partie. La fenêtre ovale primaire est encore très large et de forme irrégulière.

Le canal semi-circulaire latéral est recouvert sur toute sa longueur latérale de cartilage, lequel unit ainsi les cupules antérieure et postérieure. Les canaux semi-circulaires antérieur et postérieur ont un revêtement encore très court, qui s'unit aux cupules antérieure et postérieure.

La commissure basicapsulaire antérieure, qui relie le cartilage périotique au plan basal, est encore très faiblement développée et représentée par quelques cellules dispersées ; la

commissure basicapsulaire postérieure au contraire est bien développée.

A l'endroit où se trouve le ganglion acoustique, la paroi ventrale de la capsule auditive montre un épaississement dorsal, supportant ce ganglion (fig. 1, pl. VIII). La paroi médiale de la fenêtre ovale primaire, qui n'est pas formée par le plan basal, mais par la capsule auditive elle-même, n'est pas limitée distinctement, parce que la chondrification n'est pas achevée ; cela en explique aussi la forme bizarre. Il en est de même des parois rostrales, caudales et latérales.

Développement

On trouve pour la première fois du cartilage dans la partie ventrale de la capsule auditive future chez une larve de 6 mm. (série 6). D'abord les cupules antérieure et postérieure se chondrifient, tandis qu'on ne voit pas de cartilage autour du canal semi-circulaire latéral, excepté dans la partie rostrale autour de l'ampoule latérale. Ce cartilage se joint à celui de la cupule antérieure. La cupule postérieure se développe plus lentement que l'antérieure. Dans une larve de 6 ½ mm., le cartilage de la cupule postérieure s'est agrandi en direction médio-ventrale, sans atteindre pourtant le plan basal.

Le cartilage du canal semi-circulaire latéral dans une larve de 7 mm. (série 8) s'est accrû à partir de la partie ampullaire; dans le voisinage du sac endolymphatique les cellules cartilagineuses deviennent moins visibles. On peut suivre l'extension médio-ventrale de la cupule postérieure au-dessous de la macula succuli jusqu'au delà de la limite du ganglion VIII. Il n'y a pas encore d'union avec le plan basal. La commissure basicapsulaire antérieure n'est pas encore cartilagineuse, la commissure basicapsulaire postérieure au contraire l'est, mais est encore indépendante du plan basal.

Donc nous voyons dans la capsule auditive *deux* centres de chondrification :

1° *la cupule antérieure* qui se chondrifie la première et d'où part en direction caudale l'ébauche de la bande de carti-

lage qui entoure le canal semi-circulaire latéral, atteint la cupule postérieure et s'unit à elle.

2° *la cupule postérieure*, dont le cartilage délimite rostralement la capsule auditive et s'unit au plan basal si complètement que, dans les stades postérieurs (série 11 et 12, larves de 8 ½ et 9 ½ mm.), la limite entre eux n'est plus distincte.

Littérature

Götte (1875) a observé chez *Bombinator*, que le cartilage de la capsule auditive se montre du côté latéral, avant que la partie centrale de la base du crâne soit formée. Par sa croissance en direction axiale cette partie latérale s'unit au plan basal. C'est pourquoi Götte croit que la capsule auditive est une capsule sensorielle indépendante.

Stöhr (1882) a trouvé le premier cartilage de la capsule auditive chez *Rana* autour du canal semi-circulaire latéral ; ce cartilage commence par être indépendant du plan trabéculaire et du cartilage mésotique, mais plus tard il s'unit à eux.

La connexion membraneuse (et non pas cartilagineuse) de ce cartilage latéral avec le cartilage mésotique, l'amène à supposer que la capsule auditive est une partie du tissu mésotique, quoiqu'il soit bien forcé d'admettre que les capsules auditives des Anoures se *chondrifient* indépendamment.

Gaupp (1893) vit chez *Rana fusca* deux centres de chondrification : 1° le cartilage parachordal qui s'agrandit et limite la partie médio-ventrale, 2° le cartilage, entourant le canal semi-circulaire latéral qui croît en direction rostrale et caudale, forme les cupules antérieure et postérieure, et plus tard se fusionne par les deux commissures avec le plan basal.

Pourtant Gaupp ne put pas indiquer exactement à quel degré le cartilage périotique prend part à la limite médiale de la fenêtre ovale et où se trouve la limite entre le cartilage mésotique qui se développe à partir de la corde, et ce cartilage périotique.

PEETERS (1910) disposa de stades plus jeunes que ceux de GAUPP chez *Rana fusca* et *esculenta*; il partage l'opinion de GAUPP que le cartilage périotique ne prendrait aucune part à la formation de la limite médiale de la fenêtre ovale primaire, mais que le cartilage de cette région serait une expansion caudale du cartilage parachordal.

Une bande de cartilage, située en dehors des myotomes et en dedans de la capsule auditive, se développe d'abord et s'étend jusqu'à la limite proximale du bord de la cupule postérieure et va en avant jusqu'au plan trabéculaire.

Le cartilage de la capsule auditive se forme d'abord autour de la partie dorso-latérale du canal semi-circulaire, s'agrandit vers l'arrière et, devant la cupule postérieure s'unit à la bande ventrale, indiquée ci-dessus; de cette manière la commissure basicapsulaire postérieure se forme plus tôt que la commissure basicapsulaire antérieure.

Quand on compare les données de ces divers auteurs avec ce que nous avons vu chez *Alytes*, on trouve deux différences intéressantes :

1° Le premier développement du cartilage n'a pas lieu chez *Alytes* autour du canal semi-circulaire latéral, comme chez *Rana* et *Bombinator*. Cette différence nous frappe d'autant plus qu'il en est ainsi chez les Urodèles (STÖHR 1880, 1882 ; GAUPP 1906).

Le deuxième point, concernant l'origine du cartilage situé du côté médial de la fenêtre ovale primaire, nous intéresse davantage. Le développement chez *Alytes* montre un rapport secondaire s'établissant avec le cartilage du plan basal et fait voir un déplacement en direction orale, à partir de la cupule postérieure.

Cette observation est assez conforme à celle de GÖTTE, mais diffère de celles de STÖHR, GAUPP et PEETERS pour *Rana*.

Les données de PEETERS étant les plus précises, il est intéressant de les examiner un peu plus attentivement.

En somme, la question peut être formulée ainsi : la bande de cartilage, observée par PEETERS du côté médial de la

capsule, faut-il la considérer comme une partie du plan basal ou non ? PEETERS ne démontre pas la première supposition et à mon avis on peut considérer ce cartilage comme une partie de la capsule auditive qui se chondrifie très tôt et se rattache secondairement au cartilage qui se développe sur l'emplacement des myotomes 1 et 2 de PEETERS et forme le vrai plan basal.

S'il était exact que cette bande cartilagineuse fasse partie de la capsule auditive, alors le bord médial de la fenêtre ovale chez *Rana* serait d'origine périotique et il n'y aurait d'autres différences entre *Rana* et *Alytes* que le moment et le lieu de l'apparition du cartillage. L'observation du développement de la capsule auditive d'*Alytes* nous permet de considérer celle-ci comme une capsule sensorielle indépendante ; car la paroi capsulaire n'est pas formée d'une partie latérale et d'une autre provenant du plan basal, mais les deux centres de chondrification appartiennent à la capsule auditive elle-même.

C. Regio orbitalis

Stade I

Les trabécules cartilagineuses qui forment caudalement le plan trabéculaire non pair, ne sont pas réunies dans la région nasale par le plan internasal. On ne peut donc pas parler à ce stade d'une fenêtre basicraniale antérieure.

Caudalement comme oralement la paroi latérale est unie avec le palatocarré par l'apophyse ascendante et la commissure quadrato-craniale antérieure qui sont déjà cartilagineuses.

La partie dorso-latérale de cette paroi et la voûte crânienne sont encore membraneuses, mais dans la partie ventro-latérale on peut reconnaître du cartilage jusqu'au nerf II. Dans cette paroi latérale les deux orifices des N. III et II sont séparés l'un de l'autre par une zone encore membraneuse.

Le N. III quitte la cavité crânienne par l'angle dorso-caudal du trou oculomoteur, l'artère ophtalmique par l'angle ventro-caudal.

Le trou de l'oculomoteur est très large ; le N. III est pourtant très fin. L'orifice est en grande partie comblé par les muscles de l'œil qui s'attachent à la partie élevée du trabécule, là où arrive l'apophyse ascendante.

Le trou optique est beaucoup plus large que le nerf. Les trabécules prennent, devant le N. II, une forme plus triangulaire dont les angles aigus dorsaux et ventraux se prolongent dans la capsule membraneuse du cerveau, tandis que l'angle obtus latéral passe bientôt dans la commissure quadrato-craniale antérieure. En avant de cette commissure, les trabécules délimitent de plus en plus la partie ventrolatérale du cerveau. Le diamètre devient plus petit et la forme plus allongée, sans que les trabécules s'unissent encore par le plan internasal. Le fond ventral de la cavité crânienne est formé par une membrane qui unit les trabécules et dans laquelle on trouve des deux côtés, vis-à-vis de l'apophyse ascendante et du côté ventro-médial de la trabécule, le canal carotidien (foramen carotis primarium). Par le trou craniopalatin, qui n'est pas encore bien délimité, passe le rameau palatin de l'artère carotide interne.

Le trou du N. IV n'est pas encore visible. Le ganglion prootique est situé entre la capsule auditive et cette paroi et s'appuie en partie sur l'apophyse ascendante. Du côté dorsal, le ganglion est revêtu de la lame membraneuse du crâne qui s'unit d'autre part à la capsule auditive.

Développement

La forme en U du plan trabéculaire et des trabécules s'indique déjà à des stades non-cartilagineux par une accumulation des noyaux dans le tissu prochondral. On voit sur des coupes horizontales que les branches de l'U deviennent plus minces oralement. Elles ne sont épaisses que de quelques cellules en face des fosses nasales.

J'ai pu observer sur une larve de 5 mm. (série 4) la première formation des trabécules dans ses connexions avec le plan chordal qui est encore prochondral. La chondrification des trabécules continue en direction rostrale, en partant du plan trabéculaire. Dans une larve de 6 mm. (séries 5 et 6) on peut trouver du cartilage jusqu'à l'endroit où le N. optique croise le trabécule, tandis que dans une larve de 6 ½ mm. (série 7) elle arrive jusqu'aux environs des fosses nasales.

Dans ces trois stades (séries 5, 6 et 7), j'ai pu retrouver le rudiment des trabécules même jusqu'en avant des organes olfactifs, où il se transforme en l'ébauche des cornets. (Dans série 4 la partie distale de cette ébauche est plus ou moins diffuse).

La plus grande masse des cellules du chondroblastème des trabécules, dans une larve de 5 mm., se montre dans la partie caudale. Leur nombre diminue en direction rostrale. De ce mode de formation et de la direction de la chondrification, je crois pouvoir conclure que le rudiment des trabécules devient visible en direction orale, tandis qu'il se joint au rudiment du plan parachordal. Il est donc très probable que le plan parachordal et les trabécules ne sont pas séparés l'un de l'autre, ni à l'état prochondral, ni à l'état cartilagineux.

En même temps que le plan parachordal et les trabécules (séries 5 et 6) se chondrifient, le rebord du trabécule, auquel s'unit l'apophyse ascendante prochondrale, devient aussi cartilagineux. Dans des coupes horizontales, se succédant en direction dorsale, on voit que le contour arrondi de ce rebord, auquel s'attachent les muscles de l'œil (fig. 12, pl. IX), devient de plus en plus petit et se transforme en ébauche prochondrale du pilier de la paroi latérale ; ce pilier est la partie caudale épaissie de la paroi latérale encore membraneuse. La chondrification du rebord continue en direction dorsale de sorte que dans la série 7 (larve de 6 ½ mm.) une partie du pilier est déjà aussi cartilagineuse. Le rudiment de la paroi latérale s'unit à ce pilier (qui n'est en effet que la

partie de la paroi latérale, qui se chondrifie la première) et devient en direction rostrale moins épaisse et moins visible (fig. 11, pl. IX); la chondrification de la paroi latérale procède aussi en direction rostrale.

Dans les coupes transversales, la paroi latérale atteint sa plus grande épaisseur en son milieu ; c'est précisément là que les premières cellules cartilagineuses deviennent visibles.

Littérature

La formation des trabécules de *Rana* se fait selon Stöhr (1882) et Spemann (1898) d'avant en arrière. C'est pourquoi Spemann a vu que la formation de la commissure quadrato-craniale antérieure apparaît plus tôt que celle de l'apophyse ascendante (fig. 17, pl. 29). Le mode d'apparition du trabécule est le même chez *Triton cristatus* que chez *Rana* (Stöhr 1880 et 1882).

Quoique je n'aie pas pu examiner la *première formation* des trabécules chez *Alytes*, j'estime qu'il est très probable (p. 412) qu'elle se fait en sens inverse, c'est-à-dire caudo-rostral.

La chondrification se fait chez *Alytes* de la même manière. Quant à *Rana* je n'ai pu trouver aucune indication sur ce point.

Le pilier de la paroi latérale est chez *Alytes*, comme chez *Rana*, une continuation de la partie surélevée de la trabécule, à laquelle est unie l'apophyse ascendante. Par les données de Stöhr (1882) nous savons que cette élévation trabéculaire est plus haute chez *Rana*, moins haute chez *Pelobates* et qu'elle manque chez *Bufo* et *Hyla* (c. f. sa Taf. III, resp. fig. 21, 20 et 19). Quand on s'en tient à l'interprétation de Gaupp (1893, p. 409), que « die Seitenwandpartie nichts weiter sei als der nach oben erhöhte Trabekel selbst », il est clair que l'apophyse ascendante semble être adhérente tantôt directement au trabécule (*Bufo, Hyla*), tantôt à la paroi latérale (*Rana, Alytes*) et que le pilier de la paroi latérale tire son origine chez *Rana* et *Alytes* de la partie surélevée

du trabécule. Dans quelques coupes d'*Alytes* (fig. 2) il semble en effet que l'apophyse ascendante s'unisse à la paroi latérale. Or, l'opinion de Stöhr et de Gaupp est qu'il ne faut pas faire de distinction entre le trabécule et la paroi latérale. A mon avis, ceci est aussi fort évident dans la partie du trabécule située vis-à-vis de la commissure quadrato-craniale antérieure, qui nous montre dans les coupes transversales un profil oblong et qui limite le cerveau du côté ventro-

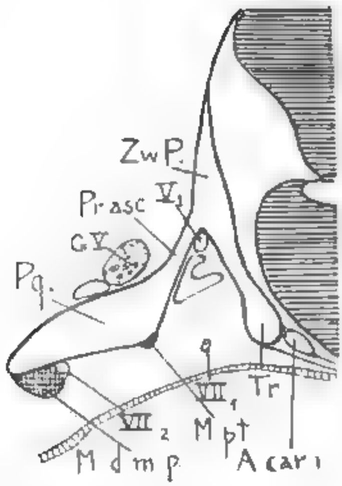

Fig. 2. — Coupe transversale d'une larve de 7 mm. (série S). *Point d'attache de l'apoph. ascendante à la paroi latérale.* Gross. 100×.
A. car. i., arteria carotis interna ; *M. d. m. p.*, musculus depressor mandibulae posterior ; *M. pt.*, musculus pterygoïdeus ; *P. q.*, palatoquadratum ; *Pr. asc.*, processus ascendens ; *Tr.* trabecula ; *Zw. P.*, pilier de la paroi latérale ; *G. V.*, ganglion prooticum ; V_1, ramus orbito-nasalis V ; VII_1 *et* VII_2, ramus palatinus et hyomandibularis VII.

latéral. La différence originelle entre les dimensions des cellules cartilagineuses du trabécule et celles des cellules de la paroi latérale, qui plus tard disparaît, peut suffisamment être interprétée par la formation précoce des trabécules et ne peut pas servir d'argument pour prouver la formation différente de la paroi latérale et du trabécule.

L'influence des trous des N. II et III aussi, ne doit pas être sousestimée comme agent ralentissant de la chondrification.

D. Regio ethmoidalis, Suprarostralia

Stade I

La forme oblongue de la coupe transversale des trabécules en face de la commissure quadrato-craniale antérieure reste la même dans la partie du trabécule qui est comprise entre le cerveau et la fosse nasale ; ici les trabécules se rapprochent l'un de l'autre et limitent le cerveau du côté ventral.

Plus loin, en direction rostrale, les trabécules reprennent à la coupe transversale leur forme ovale, dès qu'ils sont redevenus libres. Les cornes trabéculaires, situées au côté caudal du bord antérieur du cerveau, se rapprochent l'une de l'autre et se recourbent verticalement vers le bas.

Dans la partie distale des cornes il devient de plus en plus difficile de reconnaître le cartilage ; on passe peu à peu aux suprarostralia qui sont encore prochondraux. Ceux-ci se recourbent caudalement, jusqu'à atteindre le bord de la bouche, où ils s'étendent latéralement en une bande de tissu très mince qui bientôt s'élargit et se transforme en une aile triangulaire, s'étendant jusqu'à l'angle buccal. Cette partie aussi est encore prochondrale. La forme des suprarostralia se dessine clairement au milieu du tissu environnant. C'est pourquoi j'ai pu les indiquer dans le modèle (fig. 1 et 2, pl. VIII). Dans cette série il était impossible d'observer l'union médiane des suprarostralia au devant du bord de la bouche.

Les ligaments intertrabéculaires supérieur et inférieur manquent à ce stade.

Développement

J'ai pu observer la première formation des cornes trabéculaires dans une larve de 5 mm. (série 4), alors que les suprarostralia n'étaient pas encore visibles. Dans une larve

de 6 mm. (série 6) les cornes se dessinent déjà nettement, se recourbent ventralement et se transforment en tissu des suprarostralia futurs, lequel s'étend sur le bord de la bouche comme une bande de tissu de couleur foncée. Le bord de la bouche est délimité par une accumulation continue des noyaux (larves de 6 ½ et 7 mm. (séries 7 et 8)). Les deux suprarostralia sont donc unis dès leur formation.

Pendant la chondrification (larve de 12 ½ mm.) la partie centrale des suprarostralia reste très longtemps prochondrale.

Le rudiment des cornes trabéculaires se continue dans celui des suprarostralia. Plus tard, lorsque la chondrification a commencé dans les ailes latérales des suprarostralia, les deux cornes en sont séparés par une bande de tissu non-cartilagineux dans laquelle les noyaux se tassent.

Nous voyons donc que chez *Alytes* la formation des cornes trabéculaires précède celle des suprarostralia. Quant à la chondrification, elle procède de la même manière.

Les suprarostralia ont un centre cartilagineux, situé du côté latéral.

Littérature

Quand on compare les figures des stades jeunes de *Bombinator* (Götte, 1875, Taf. XVIII, fig. 123) et de *Rana* (Stöhr, 1882, Taf. III, fig. 18 ; Gaupp, 1893, Taf. XIII, fig. 1) avec mon modèle du crâne d'une larve d'*Alytes* de 7 mm., on remarque que chez ceux-là le plan internasal s'est formé avant ou en même temps que le plan trabéculaire non accouplé soit achevé. Chez *Alytes* nous voyons le plan internasal se développer plus tard (9 ½-12 ½ mm.), tandis que le plan basal existe depuis longtemps.

La connexité génétique des cornes avec les suprarostralia fut observée par Stöhr (1882) et Spemann (1898) chez *Rana*. Le premier conclut que les suprarostralia se sont dégagés des cornes trabéculaires et croit qu'il est prouvé que les suprarostralia ne seraient qu'une partie antérieure des cornes, modifiée.

SPEMANN n'est pas du même avis. Il dit avec raison que la continuité de deux formations prochondrales ne permet pas de conclure à une véritable unité génétique. L'hyoide, par exemple, de *Rana* est à son origine en continuité avec le quadratum.

L'observation de SPEMANN chez *Rana*, que le rudiment des suprarostralia se montre déjà comme une petite accumulation des cellules compactes, avant qu'on puisse voir les trabécules, nous suggère l'idée que les suprarostralia pourraient bien être plus ou moins indépendants. Le centre cartilagineux latéral indépendant, qu'on trouve ainsi chez *Alytes*, nous offre pour cela un argument de plus.

La formation des cornes trabéculaires apparaît chez *Alytes*, contrairement à ce que l'on voit chez *Rana*, *avant* celle des suprarostralia, tout en étant en connexion entre eux ; les trabécules deviennent cartilagineux d'abord. On pourrait prendre cette observation comme un argument prouvant l'unité génétique des suprarostralia et des cornes trabéculaires, s'il ne fallait pas tenir compte des premières phases du développement des embryons d'*Alytes*, lesquels diffèrent de celles des autres Anoures (¹).

Nous y voyons, contrairement à *Rana*, que la partie rostrale du crâne ne se développe pas si vite que la partie caudale. Chez *Rana* cette région orale montre un développement avancé et il semble que cette formation précoce soit en rapport avec la fonction précoce des mâchoires. On ne peut donc pas affirmer que le développement des suprarostralia chez *Alytes* soit plus primitif que celui de *Rana*. Il est probable que les suprarostralia ne sont que des parties des cornes trabéculaires, modifiées par la vie larvaire et le développement des mâchoires.

Une deuxième différence entre *Alytes* et *Rana* c'est que les suprarostralia et les mâchoires du premier s'unissent entre

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(¹) VOGT (1842, cité selon HÉRON-ROYER et VAN BAMBEKE, 1889) donne la même interprétation de la formation ralentie des mâchoires cornées chez *Alytes*.

eux dans le plan médian; grâce à la chondrification caudo-latérale-rostromédiale, la pièce médiane reste longtemps prochondrale. Les suprarostralia de *Rana* au contraire sont formés séparément (Stöhr, 1882).

Les mâchoires cornées chez cette espèce commencent aussi par être séparées l'une de l'autre (Héron-Royer, 1889 ; Gaupp, 1893, 1906), quoique Peeters (1910) ne pût s'en convaincre. Le rudiment des mâchoires cornées d'*Alytes* (larve de 9 ½ mm., série 13) n'est pas pair.

La formation lente des suprarostralia d'*Alytes* nous explique pourquoi l'histoire de leur développement ne montre plus leur séparation initiale.

F. Palatoquadratum, Cartilago Meckeli, Infrarostralia

Stade I

Le *palatocarré* est uni par du cartilage au trabécule par l'apophyse ascendante et la commissure quadrato-craniale antérieure. L'apophyse musculaire est bien développée.

La fenêtre suboculaire a pris à peu près la forme d'un triangle rectangle, dont les côtés sont limités par le trabécule et l'apophyse ascendante. La membrane suboculaire manque.

Il n'y a pas d'union entre le palatocarré et la capsule auditive ; le bord caudal du premier se trouve dans le même plan transversal que le bord antérieur de la seconde.

Le point d'attache du palatocarré et de l'hyoide se trouve dans la partie aplatie du premier, à la hauteur du bord rostral du trou de l'oculomoteur, donc environ à un tiers de la longueur du palatocarré, à compter depuis son bord caudal. Une fente articulaire n'existe pas encore ; l'union se fait par un tissu de couleur foncée avec des noyaux compacts.

La partie articulaire est encore très courte. Un peu en avant du bord antérieur de la commissure quadrato-craniale antérieure on voit la cavité articulaire du cartilage de Meckel.

Le *cartilage de Meckel*, transversal, nous montre du côté caudo-latéral une saillie, qui entoure la partie articulaire du quadratum. Le cartilage est encore très jeune.

A peu près vis-à-vis du centre du bord antérieur du cartilage de Meckel, on trouve des deux côtés les rudiments de deux pièces cartilagineuses, nommées par PEETERS (1910) « paramandibularia ». Ils sont unis au cartilage de Meckel.

Les *infrarostralia* sont au même stade du développement que le cartilage de Meckel et sont unis à lui par un tissu pointillé de noyaux; ils ont leur propre centre de chondrification et sont bien délimités vis-à-vis du cartilage de Meckel, quoiqu'il n'y ait pas encore de fente articulaire. Les deux infrarostralia sont unis du côté caudal sur la ligne médiane par une bande de tissu de couleur foncée, visible sur quelques coupes transversales. C'est un tissu d'union particulier qui continue à se développer et dans lequel une copule cartilagineuse se formera plus tard (c. f. le stade II).

Développement

Il m'a manqué des séries pour l'étude de la première ébauche du palatocarré, du cartilage de Meckel et des infrarostralia. Dans la série 3 (larve de 5 mm.) le palatocarré, ainsi que le squelette viscéral, se dessine indistinctement par des amas de noyaux. Le rudiment du palatocarré apparaît clairement dans la série 4 (larve de 5 mm.), mais on y aperçoit déjà les deux unions avec les trabécules. Le cartilage de Meckel et les infrarostralia sont aussi en train de se former. Ils se voient dans la série 5 (larve de 6 mm.) comme une bande continue de tissu, de couleur foncée, dans laquelle on peut reconnaître, dans des coupes horizontales, la forme des composants.

Sur la ligne médiane les ébauches des infrarostralia sont réunies par une bande de tissu de forme ovoïde dont la base se prolonge caudalement.

Le rudiment des « paramandibularia » fut constaté pour la première fois dans une larve de 7 mm. (série 9).

La chondrification du palatocarré se fait en direction rostrale. L'apophyse ascendante et la commissure quadratocraniale antérieure qui, dans une larve de 7 mm. (série 8), ne sont pas encore cartilagineuses, semblent se transformer en cartilage à peu près en même temps (série 9).

Le cartilage de Meckel et les infrarostralia ont chacun leur centre de chondrification.

Littérature

La continuité du palatocarré, du cartilage de Meckel et des infrarostralia dans leur formation primitive fut observée déjà par Stöhr (1882) et Spemann (1898) chez *Rana*; de même ils ont vu les entailles qui les séparent et les centres cartilagineux indépendants. Götte (1875) put constater la même chose chez *Bombinator*.

Les infrarostralia d'*Alytes* sont unis par un tissu pointillé de noyaux et de couleur foncée, dans lequel on trouvera plus tard une copula cartilagineuse (c. f. le stade II).

Chez *Rana esculenta* (6,5 mm.) Peeters (1910) a observé déjà très tôt un lien *cartilagineux*; à aucun stade il ne vit les deux moitiés séparées l'une de l'autre.

Les deux remarquables pièces de cartilage que Peeters (1910) trouva dans des larves d'*Alytes* de 43 mm. des deux côtés des infrarostralia devant le cartilage de Meckel, sont nommés par lui « paramandibularia ». Il les appela ainsi en suivant la nomenclature de Fürbringer (1904). Celui-ci trouva deux paires de pièces cartilagineuses chez *Protopterus* et chez *Lepidosiren*, qui se développent indépendamment du cartilage de Meckel. La paire orale s'unit dans le cours du développement à ce cartilage, tandis que la caudale reste libre. L'isolement permanent des pièces cartilagineuses chez *Alytes* vis-à-vis du cartilage de Meckel est la raison pour laquelle Peeters les compare à la paire de paramandibularia postérieure des Dipnoï.

J'ai reconnu les paramandibularia d'*Alytes* pour la première fois au stade I (larve de 7 mm.).

Contrairement au cartilage de Meckel ils ne sont pas encore cartilagineux et apparaissent comme une condensation de noyaux. Il m'a été impossible de constater leur indépendance initiale, mais j'ai pu observer dès ce stade que le cartilage de Meckel et les paramandibularia se touchent. Cependant l'origine de ces pièces cartilagineuses ne nous suggère pas l'idée qu'ils tirent leur origine du cartilage de Meckel et leur chondrification retardée (larve de 12-16 ½ mm.) prouve même une certaine indépendance. Dans des séries postérieures les rapports des cartilages de Meckel avec les paramandibularia se retrouvent toujours ; ils sont unis par une sorte de tissu périchondral (c. f. le stade II).

Pour ces raisons, il me semble que les paramandibularia pourraient plutôt être comparées aux pièces de cartilage orales des Dipnoï, dont j'ai parlé plus haut, quoiqu'elles ne subissent pas de concrescence avec le cartilage de Meckel chez *Alytes*.

En tout cas il ne me semble pas recommandable de nommer ces pièces cartilagineuses d'*Alytes* « paramandibularia » parce que FÜRBRINGER lui-même, chez les *Dipneustes*, ne veut employer ce nom que sous réserve (1).

Une comparaison avec les cartilages des lèvres inférieures des Sélaciens, ainsi que PEETERS l'a déjà indiquée, est tout aussi possible. Car GAUPP a dit avec raison (1906), (p. 588) : « Genetische Kriterien zur Charakteristik der praekranialen Skelettheile fehlen bisher, und die diesbezüglichen Vergleiche sind noch unsicher ».

Tout bien considére il vaut mieux ne pas donner par l'emploi du mot « paramandibularia » l'impression, que l'homologie avec les cartilages du même nom des Dipnoï est établie. Pour moi, je préfère remplacer ce terme par « *admandibularia* », ce qui exprime en même temps leurs rapports avec les cartilages de Meckel.

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(1) FÜRBRINGER (1904, p. 481) dit à cet égard : « Sollte die Untersuchung an jüngeren Stadien eine getrennte Entstehung (du cartilage de Meckel et des paramandibularia) an der ich noch Zweifel hege, zeigen, so wäre dann ein besonderer Name, wie etwa Paramandibularia, zu empfehlen».

IV. SUITE DU DÉVELOPPEMENT DU CHONDROCRANE AVANT LA MÉTAMORPHOSE JUSQU'AU STADE II INCLUS

A. Planum basale, Arcus occipitalis, Chorda dorsalis

Stade II

(larve de 53 mm.; longueur de la queue 31,5 mm , longueur des pattes postérieures 3 mm., série 19).

Au premier stade on observe un bord crânial distinct du plan basal, mais ce bord disparaît parce que la fenêtre basicraniale antérieure s'est fermée. La limite latérale vis-à-vis de la capsule auditive n'est pas non plus visible et la limite caudale n'est pas si nette qu'on pourrait s'y attendre. A l'endroit où les arcs occipitaux se recourbent latéralement en haut, on aperçoit du côté dorsal de la corde, un tissu qui s'unit crânialement au cartilage du plan basal, tandis qu'il se prolonge caudalement dans la partie épicordale de la colonne vertébrale. Il se distingue du cartilage du plan basal par le grand nombre de noyaux accumulés et entourés d'une substance intercellulaire assez peu développée. Ce tissu donne l'impression d'être un tissu connectif en train de se chondrifier et qui tire son origine de la couche squelettogène qui entoure la gaîne secondaire de la corde.

Le *plan basal* montre une épaisseur remarquable sur toute sa longueur. La partie caudale est voûtée ; dans le voisinage du trou acoustique il devient plus aplati. En direction plus crâniale il devient creux à cause de la situation dorso-rostrale de l'hypophyse. Ainsi s'établit une transition avec le fond du crâne cartilagineux qui est encore très mince.

Les *arcs occipitaux* s'élèvent à peu près dans un plan transversal, tandis que leurs parties proximales sont recourbées un peu en direction caudale. C'est avec cette partie de l'arc

occipital, que le premier arc vertébral s'articulera plus tard. La partie distale de l'arc occipital s'unit à la capsule auditive par la crête occipitale latérale et délimite ainsi le trou jugulaire.

A l'intérieur du crâne les côtés dorsal et ventral de la *corde* sont entourés de cartilage ; seule la partie située en arrière du trou jugulaire n'a pas de revêtement cartilagineux. La corde disparaît un peu au devant du bord antérieur du trou périlymphatique interne. La corde volumineuse se termine assez brusquement en pointe dans le crâne (cf. fig. 3 et 4, pl. VIII, pour un stade plus jeune).

Développement

Au stade I le bord antérieur du *plan basal* limitait le côté caudal de la fenêtre basicraniale antérieure. Pendant le développement cette limite disparaît par la fermeture de cette fenêtre, tout comme le font les limites vis-à-vis des capsules auditives. Le bord caudal est bien distinct et séparé par le tissu occipito-vertébral du rudiment de la partie basale du premier arc vertébral, qu'on peut observer chez des larves de 15 à 16 mm.

L'*arc occipital* qui s'élève d'abord en direction caudo-latérale, prend par l'agrandissement du plan basal une position plus transversale. La crête occipitale latérale manquant d'abord, on voit chez des larves de 9 ½ et 12 mm. l'arc occipital se joindre directement à la capsule auditive. Le développement de cette crête se montre pour la première fois dans des larves de 16 mm. et comme chez Rana. Une incisure occipitale dans laquelle la base du premier arc vertébral se prolonge, ne se développe pas ou à peine chez Alytes.

Mes observations concernant la réduction de la corde d'Alytes se résument ainsi : Le bout extrême et courbé de la corde [1] disparaît le premier, car il est absorbé par le car-

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[1] Je laisse ici de côté la réduction très précoce du bout de la corde, dont j'ai parlé aux pages 388 et 405.

tilage du plan basal. Ensuite se manifeste la compression latérale, causée par la croissance du cartilage latéral du plan basal, tandis que en même temps ce bout se couvre de cartilage du côté dorsal. Le cartilage ventral se développe plus tard. La compression du bout de la corde en fait disparaître les éléments vivants et enfin les gaînes secondaires et primaires sont absorbées dans le plan basal.

Littérature

On ne peut pas constater de différences importantes dans la partie caudale du crâne de *Rana*, de *Bombinator* et d'*Alytes* avant la métamorphose.

La crête occipitale latérale finit par se développer chez *Alytes* tout aussi bien que chez *Rana* ; la concrescence précoce empêche de voir si cette crête provient de la capsule auditive ou de l'arc lui-même. Selon la description de GAUPP (1893), la crête occipitale latérale se développe chez des larves de *Rana fusca* d'une longueur de 14 à 29 mm. comme une bordure cartilagineuse qui prend son origine à mi-hauteur de la capsule auditive et qui relie celle-ci à l'arc occipital. L'arc occipital de *Rana* ne se rattache pas directement à la capsule auditive, comme c'est le cas chez *Alytes*. On peut expliquer cette différence par le développement précoce de l'arc occipital chez celui-ci.

Chez *Alytes* également la formation de la crête nous donne l'impression qu'elle est due à un épaississement de la paroi de la capsule auditive.

PEETERS (1910) a déjà signalé que l'incisure occipitale d'*Alytes* manque à peu près complètement.

La réduction de la corde se fait d'une façon analogue à celle de *Bombinator* et de *Rana*. GOETTE (1875) et GAUPP (1893) décrivent une réduction en trois parties : 1° la partie antérieure qui est comprimée latéralement ; 2° une partie centrale qui se chondrifie ; 3° une partie qui est rejetée du côté ventral du plan basal ; ces deux derniers modes de réduction ont lieu pendant et après la métamorphose et peuvent être

laissés de côté (1). La description de la réduction et de la compression de la partie antérieure de la corde par les auteurs nommés est aussi valable pour *Alytes*.

B. Capsula auditiva. Tectum posterius

Stade II

En décrivant la *capsule auditive* c. a., je veux seulement souligner les différences avec *Rana*. On peut renvoyer pour le reste à la description de GAUPP (1893, p. 307) du second stade de *Rana*.

Maintenant l'organe auditif est tout à fait entouré d'une solide capsule de cartilage et séparé par une cloison médiane de la cavité cranienne. Les canaux semicirculaires sont entourés de cartilage. La fenêtre ovale a pris sa position latérale et sa forme elliptique ; l'operculum en couvre la partie caudale, la pars interna plectri nous montre déjà un commencement de chondrification.

Le trou périlymphatique accessoire manque (2).

Les troux périlymphatiques supérieur et inférieur (interne et externe, PEETERS) ont une position analogue à celle de *Rana*.

Le trou acoustique s'est divisé en trou acoustique antérieur et postérieur.

Le nerf facial et le nerf auditif entrent dans la capsule auditive par un canal. Comme le trajet intracapsulaire du nerf facial des Anoures est assez mal connu (3), je le décrirai en détail, à l'aide de la figure semi-schématique 3.

Le nerf VIII d'*Alytes* possède comme d'ordinaire un rameau postérieur et antérieur. Ce nerf auditif, la racine dorsale et la racine ventrale du nerf facial, prennent leur origine au même endroit. Les deux dernières se dirigent avec le ra-

(1) *Alytes* ressemble aussi à cet égard à *Rana*.

(2) Je ne l'ai vu dans aucune série d'*Alytes*.

(3) GAUPP (1911) ne parle qu'en passant d'un canal du nerf facial chez *Bombinator* et *Alytes*.

meau antérieur VIII en direction rostrale, après avoir fourni le rameau postérieur VIII (fig. 3, *a*, *b* et *c*).

Vis-à-vis de l'origine du N. V. la racine dorsale du N. VII devient libre et court à l'intérieur du crâne (fig. 3, *c* et *d*). Le rameau antérieur VIII reste uni à la racine ventrale du N. VII, tandis que la position médiale de ce dernier appa-

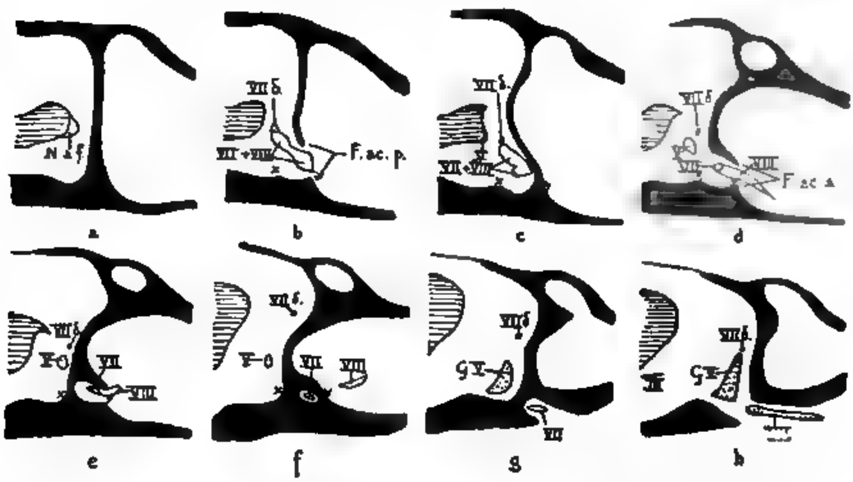

FIG. 3 *a-h*. — Coupes transversales d'une larve de 53 mm. (série 19) ; elles commencent vis-à-vis du tectum synoticum et se succèdent en direction rostrale. Gross. 13×.

Figures schématisées pour expliquer le cours du nerf VII.

F. ac. a., et *F. ac. p.*, foramen acusticum anterius et posterius ; *G. V.*, ganglion nervi trigemini ; *N. a. f.*, nervus acustico-facialis ; *III, V, VII, VIII*, nervus oculomotorius, etc. ; *VIId*, racine dorsale du nerf facial.

raît nettement grâce à l'accumulation des noyaux. Tous deux entrent dans la cavité de la capsule auditive par le trou acoustique antérieur (fig. 3 *d*), qui est justement situé devant et sous le trou d'entrée du canal endolymphatique.

La cloison qui sépare les trous acoustiques postérieur et antérieur ne se trouve pas dans le même plan que la cloison médiale de la capsule auditive, mais se dresse sur une partie du fond de la capsule auditive, un peu plus en dedans. Une coupe transversale par le trou acoustique postérieur montre

le point *x*, où le bord antérieur du trou acoustique (primitivement cloison médiale de la capsule auditive) se relèvera et le point *y*, c'est-à-dire le point de contact entre la cloison des trous acoustiques postérieur et antérieur (développée plus tard) et le fond de la capsule auditive (fig. 3, *b*, *c*, *e*).

Le bord dorsal du trou acoustique antérieur s'est fort élargi, car il n'est pas placé dans un plan vertical, mais se recourbe dans la cavité de la capsule auditive (fig. 3 *d*). Cette espèce de bordure se prolonge en direction orale après la fermeture du trou acoustique sous forme d'un bord large, sous lequel passent le rameau antérieur VIII et la racine ventrale du nerf facial (fig. 3 *e*). Le rameau antérieur VIII devient bientôt libre et se dirige vers les parties intérieures de l'organe auditif. Le nerf facial est enfermé dès lors dans un canal, parce que le rebord rencontre le fond de la capsule auditive sur le prolongement du point *y* (fig. 3 *f*). Les parois de ce canal se composent des éléments suivants : 1° une partie horizontale, provenant de la paroi ventrale de la capsule auditive et du plan basal ; 2° une partie verticale, provenant de la cloison médiale de la capsule auditive ; 3° une petite cloison oblique, correspondant par sa position à la cloison qui sépare les trous acoustiques postérieur et antérieur.

Cette cloison oblique s'épaissit en direction orale et passe successivement dans la capsule auditive elle-même, tandis que le nerf se recourbe de plus en plus en direction ventrale. La cloison horizontale au contraire disparaît peu à peu ; par conséquent le nerf facial se trouve bientôt libre en dehors de la capsule auditive et peut alors s'unir au ganglion V (fig. 3 *g* et *h*), après que la cupule antérieure s'est éloignée du plan basal.

Il faut donc distinguer la cloison de la capsule auditive verticale, médiale, — qui entoure le trou périlymphatique supérieur et le trou acoustique primaire, non-divisé, — de la petite cloison, qui divise celui-ci en deux orifices et qui se prolonge dans la cloison séparant le nerf auditif du nerf facial et de la capsule auditive. Par rapport à la cloison verticale

le nerf facial (racine ventrale) court sur son côté latéral ; chez *Rana* au contraire sur son côté médial.

A ce stade le nerf facial semble ne pas entrer dans les cavités de la capsule auditive, mais l'histoire du développement nous apprendra qu'il y pénètre tout de même.

Le *tectum posterius* unit les deux capsules auditives et ne possède pas de taenia tecti medialis, comme chez *Rana*. A aucun stade, ni pendant la métamorphose, on ne peut l'observer chez *Alytes*. Des taeniae tecti marginales libres manquent aussi chez *Alytes*, quoiqu'on puisse trouver au côté médio-dorsal des capsules auditives des bordures, qui prennent leur origine du tectum posterius et qui formeront le substratum cartilagineux des pariétaux, lesquels sont déjà présents dans ce stade. On pourrait plutôt nommer ces bordures *cristae marginales*, parce que le développement nous montrera qu'elles ne sont jamais indépendantes chez *Alytes*,

A gauche la crista parotica est visible comme un épaississement rostro-latéral de la paroi de la capsule auditive, à droite cela ne se dessine pas si nettement.

Développement

La *capsule auditive*, qui au premier stade (fig. 1 et 2, pl. VIII), était peu développée, se recouvre très vite de cartilage de toutes parts. Déjà dans une larve de 12 ½ mm. il en est ainsi et la cloison médiale est formée. Faute de séries nécessaires (entre 9 ½ et 12 ½ mm.), je suis forcé de décrire sommairement ces processus.

Les cartilages des cupules antérieure et postérieure poussent l'un vers l'autre pour former le toit et se joignent bientôt au cartilage qui part du canal semicirculaire latéral en direction dorso-médiale, La partie de la cloison médiale, située entre le trou du N. VIII et le trou périlymphatique interne, se chondrifie d'abord et est bientôt suivie par les parties qui touchent la cupule antérieure et postérieure. Au début il reste une seule grande ouverture qui entoure le trou acoustique et le trou pour le canal endolymphatique. Le

canal semicirculaire latéral s'enveloppe de cartilage, partant de la cupule antérieure et se dirigeant en direction caudale ; puis et dans le même sens, le canal antérieur suit, et peu après enfin le canal postérieur, mais en direction opposée.

Les trous périlymphatiques supérieur (internum) et inférieur (externum) ne sont entourés de cartilage que dans une larve de 22 mm.

J'ai observé le développement des cavités périlymphatiques [1] dans une larve de 16 mm. (série 15) et en même temps le rudiment de la petite cloison qui limitera du côté caudal le trou périlymphatique supérieur. A ce stade, on voit la connexion du recessus partis neglectae du canal périlympha-

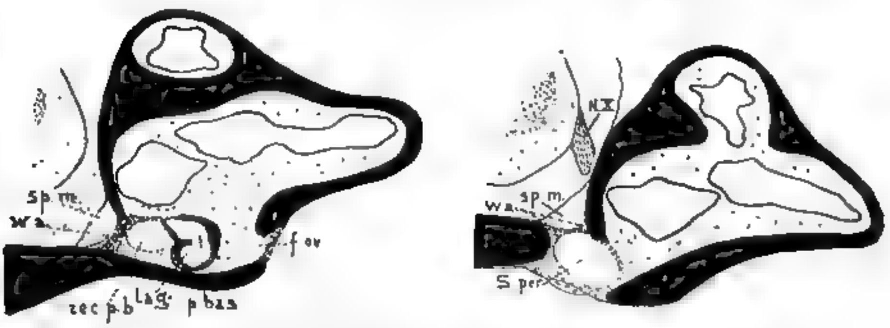

FIG. 4 *a* et *b*. — Coupes transversales à travers la capsule auditive d'une larve de 16 mm. (série 15). Gross. 50×.

f. ov., fenestra ovalis ; *lag.*, lagena ; *p. bas.*, pars basilaris ; *rec. p. b.*, recessus partis basilaris ; *s. per.*, saccus perilymphaticus ; *sp. m.*, spatium meningeale; *w. a.*, formation de la paroi située au bord caudal du foramen perilymphaticum internum.

Dans la figure *b* on voit la position du foramen perilymphaticum externum.

tique et de l'espace meningé, tandis que le recessus partis basilaris, séparé de ces cavités est lié au sac périlymphatique. Il n'y pas de communication entre le « spatium meningeale » et le sac périlymphatique. Le recessus partis basilaris, situé en dedans de la capsule auditive et le spatium meningeale

[1] Pour la terminologie, appliquée ci-dessous, on peut comparer: HARRISON (1902).

dans le cavum cranii, se touchent et c'est dans ce plan de contact que la nouvelle cloison va se former (fig. 4*a*). Cette cloison se trouve dans le même plan que la cloison médiale de la capsule auditive et s'unit du côté caudal du trou acoustique au cartilage de cette capsule. Lorsque cette cloison s'est chondrifiée sur une larve de 22 mm. (fig. 5*a*) on peut

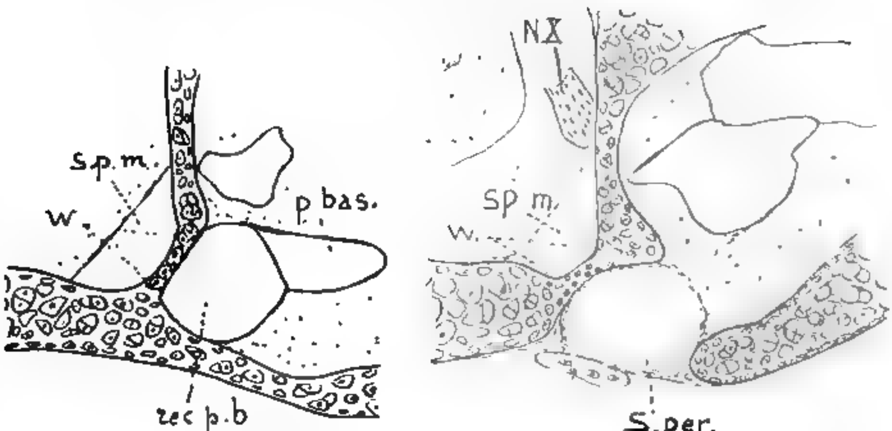

FIG. 5 *a* et *b*. — Coupes transversales à travers la capsule auditive d'une larve de 22 mm. (série 16). Gross. 95×.

A présent, la paroi, située au côté caudal du for. peri. int. s'est transformée en cartilage. Dans la figure b la position du for. peril. ext. est à voir.

p. bas., pars basilaris ; *rec. p. b.*, recessus partis basilaris ; *s. per.*, saccus perilymphaticus ; *sp. m.*, spatium meningeale.

discerner pour la première fois un trou périlymphatique supérieur (interne). Ce trou est donc un orifice dans la cloison capsulaire *médiale*, lequel est limité par du cartilage à son côté caudal après la formation du canal périlymphatique.

Chez la larve de 16 mm. on peut aussi observer comment se forme le trou périlymphatique inférieur. La figure 4*b* représente une coupe de cette larve, exécutée dans une partie plus caudale que celle de la fig. 4*a*. La capsule auditive s'est éloignée du plan basal et nous montre à l'extérieur une ouverture médio-ventrale, dans laquelle le sacculus est contenu en partie. Ceci est le trou périlymphatique inférieur ; une

larve de 22 mm. nous le rendra plus clair. La cloison limitant le bord postérieur du trou périlymphatique supérieur, s'est chondrifiée (fig. 5*b*) et a uni la capsule auditive au plan basal en direction caudale sur une grande distance. On peut suivre cette cloison en arrière jusqu'au point où le sac périlymphatique et le spatium meningeale sont unis par le ductus reuniens, c'est-à-dire jusqu'au trou jugulaire. Donc le trou périlymphatique inférieur est une partie de la cloison de la capsule auditive qui ne se chondrifie pas, probablement à cause du recessus partis basilaris et du sac périlymphatique qui sont fort développés.

Le trou acoustique est d'abord uni à l'orifice du canal endolymphatique. On peut trouver cela chez une larve de 16 mm. Dans une larve de 22 mm., les deux orifices sont séparés par une cloison cartilagineuse horizontale.

La formation d'un trou acoustique divisé en deux pour les rameaux antérieur et postérieur du N. VIII, se fait dans des larves de 29 à 53 mm.

L'orifice pour le N. VII est déjà visible dans la cloison de la capsule auditive sur une larve de 9 ½ mm. On peut très distinctement observer ici que le nerf facial et le rameau antérieur du N. VIII entrent dans la capsule auditive et qu'ils sont situés au côté latéral de la cloison médiale qui est encore membraneuse à ce stade et sépare ces nerfs de l'origine du N. V. La cloison capsulaire médio-ventrale membraneuse est percée par le nerf facial, ce que l'on peut observer aussi sur une larve de 12 ½ mm., dans laquelle le trou se trouve précisément à l'endroit où le plan basal et la capsule auditive se touchent. Dans une larve de 16 mm, la disposition est un peu modifiée parce que le développement de la cloison médiale est plus avancé et le trou acoustique est maintenant limité du côté rostral par du cartilage. Cette cloison cartilagineuse sépare l'origine du N. V. d'avec le N. VII. Le nerf facial court d'abord le long du côté latéral de cette cloison ; mais à l'endroit où la cupule antérieure s'éloigne du plan basal et où le nerf facial quitte la capsule auditive, ce nerf est entouré par : le plan basal, la cloison

de la capsule auditive médiale et la ventrale (fig. 6). A ce stade nous ne voyons qu'un seul canal rudimentaire, dont le

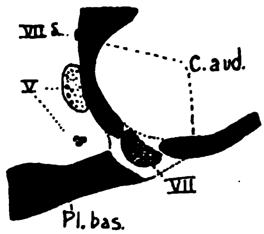

FIG. 6. — Coupe transversale à travers la cupula anterior et le plan basal d'une larve de 16 mm. (série 15). Gross. 45×.
Situation du N. VII (partie ganglionnaire) entre le plan basal Pl. bas.) et la capsule auditive (C. aud.). On peut se figurer la formation de la partie extra-capsulaire du canal facial en les unissant selon les lignes pointillées.

premier développement se manifeste dans une larve de 25 mm. La plus petite partie de ce canal, c'est-à-dire la partie orale est formée par la croissance du plan basal en direction rostrale et latérale. C'est pourquoi le trajet du nerf est très court entre le plan basal et la capsule auditive. On peut se représenter cette disposition en reliant dans la figure 6 les cloisons par les lignes pointillées. La plus grande partie du canal est due à une formation cartilagineuse en dedans de la capsule auditive elle-même. Par conséquent la figure 3*f* ne nous

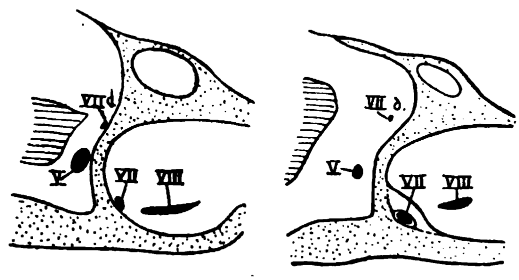

FIG. 7 *a* et *b*. — Coupes transversales à travers la capsule auditive d'une larve de 25 mm. (série 17) et d'une larve de 53 mm. ; celle-ci est la même que nous montre la fig. 3 *f*. Gross. 28×, resp. 15×.
Formation du canal facial à l'intérieur de la capsule auditive. Dans la figure b la paroi cartilagineuse, nouvellement formée, n'est pas pointillée comme le reste du cartilage.

montre pas le point où le nerf se trouve entre la capsule auditive et le plan basal, mais bien comment se forme le canal à l'intérieur de la capsule auditive. Une comparaison entre les séries 17 et 19 éclaircira ce détail. La figure 7*a* est une coupe transversale de la série 17 (larve de 25 mm.), prise à peu près à la même hauteur que celle de la figure 3*f*. Dans cette larve de 25 mm. le nerf est encore libre en dedans de la capsule auditive et sans revêtement cartilagineux. Dans la figure 7*b* (correspondante à la figure 3*f*) la position de la cloison capsulaire originelle est figurée par un pointillé et l'on voit clairement que le nerf se trouve dans la capsule auditive, bien que séparé de la cavité capsulaire par la cloison cartilagineuse (non-pointillée dans le dessin) qui vient de se former. A mesure que la capsule auditive s'agrandit, le canal se prolonge en direction caudale, de sorte que dans la série 21 (larve de 55 mm.) le nerf facial s'engage presque immédiatement dans son canal dont le revêtement cartilagineux est d'origine dorsale.

Ce que je viens de dire prouve que le point *y* dans la figure 3 est situé en dedans de la capsule auditive et que la cloison séparant les deux trous acoustiques est différente de la cloison capsulaire médiane qui se développe d'abord.

En résumé on peut dire que le nerf facial perce la cloison de la capsule auditive et qu'il est enfermé ensuite dans un canal dont la partie rostrale, très petite, est formée par la capsule auditive et le plan basal, tandis que la partie la plus longue doit son origine au revêtement cartilagineux qui se développera plus tard en dedans de la capsule auditive.

La fenêtre ovale qui au premier stade est encore très large et irrégulière, se ferme en direction rostro-caudale et médio-latérale.

La limite médio-ventrale, sur une larve de 12 ½ mm., n'est pas encore nette, parce que le cartilage passe successivement dans la membrane, riche en noyaux, qui en recouvre l'ouverture. Dans une larve de 16 mm., la fenêtre a pris sa forme ovale et est limité distinctement de tous côtés. Ses dimensions augmentent avec l'accroissement des larves.

On trouve l'ébauche du *tectum posterius* dans une larve de 12 ½ mm., dans laquelle les parties latérales, qui touchent la capsule auditive et se trouvent juste au côté caudal du canal endolymphatique, sont cartilagineuses. La partie centrale n'est pas encore chondrifiée et se compose d'un tissu prochondral, à noyaux allongés. Le cartilage latéral se prolonge dans la voûte cartilagineuse du sinus supérieur.

Une larve de 16 mm. nous montre une particularité que j'ai pu constater plus d'une fois : le développement est plus avancé d'un côté que de l'autre. A gauche, la partie cartilagineuse centrale du tectum posterius est unie avec le cartilage latéral, tandis que à droite ils sont séparés par une bande de tissu encore membraneux. Il est donc très probable que la partie centrale se développe indépendamment des parties latérales. Je n'ai pas pu vérifier objectivement ce point faute de séries convenables. Dans une larve de 23 mm. le tectum posterius est tout à fait cartilagineux.

A aucun stade on ne trouve de taenia tecti medialis.

Les cristae marginales se développent en direction rostrale et médiale, en rapport avec les parties latérales du tectum posterius et se prolongent dans la paroi latérale du crâne. Elles ne sont jamais indépendantes de la capsule auditive, comme chez *Rana* et on ne peut donc pas les nommer des « taeniae ».

Littérature

Gaupp (1893) a décrit la chondrification de la capsule auditive. J'ai déjà indiqué que les centres de chondrification chez *Alytes* ne sont pas, comme chez *Rana*, le cartilage mésotique, ni le cartilage périotique. Chez *Rana fusca* la chondrification ne procède pas régulièrement à partir de ces deux points, mais bien, selon Gaupp, de certains centres, par exemple, le rebord qui, au côté médio-dorsal des canaux demicirculaires, joint les deux cupules l'une à l'autre. Ce cartilage formera le toit et une partie de la cloison médiale.

Peeters (1910) au contraire a observé que la voûte du canal antérieur du sinus postérieur et du canal postérieur

se chondrifie en dernier lieu. Le cartilage croît à partir du canal latéral en direction médiale, en couvrant la voûte jusqu'au bord latéral des canaux antérieur et postérieur ; de même, un rebord se développe au côté médial du sinus supérieur et des canaux antérieur et postérieur. A partir de ces rebords le sinus et les canaux se chondrifient.

Cette description de PEETERS concernant *Rana fusca* est exacte pour *Alytes* autant que je pus l'observer.

Les trois canaux demi-circulaires de *Rana*, d'*Alytes* et des autres Anoures, y compris *Pipa* et *Xenopus*, s'entourent de cartilage. Au contraire chez les Urodèles le septum posterius souvent ne se développe pas (OKAJIMA, 1911*a*) (1). *Necturus* (PEETERS, 1910) *Hynobius* et *Onychodatylus* (OKAJIMA, 1911*a*) sont des exceptions à cette règle, quoique chez les deux derniers le septum posterius manque parfois (2). Puisque le canal postérieur se forme le dernier pendant le développement de l'organe auditif membraneux, il est compréhensible qu'il s'entoure aussi de cartilage le dernier (OKAJIMA, 1912). Le fait que chez les Anoures le septum posterius se forme après les septa anterius et laterale, s'accorde avec ce mode de développement. Aussi puisque le septum manque généralement chez les Urodèles, il est, comparé aux septa anterius et laterale, le dernier des trois dans la phylogénie.

Longtemps on a considéré l'existence d'un seul orifice périlymphatique comme la caractéristique des Urodèles. Mais depuis les recherches de OKAJIMA (1911*b* et 1912) cela n'est plus exact. Dans les stades larvaires de *Hynobius* on ne trouve qu'un seul orifice dans la cloison capsulaire médiale ; mais plus tard on en voit deux, situés l'un derrière l'autre (orifices périlymphatiques antérieur et postérieur). Par le développement de la portion basiliaire, le recessus partis basilaris se sépare du canal périlymphatique. Une bande de tissu connectif, étendue dans le trou entre ce récessus et le canal

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(1) PEETERS (1910) trouva chez Triton seulement le septum anterius ; GAUPP (1906) au contraire, vit aussi le septum laterale.

(2) Parmi les Gymnophiones, Ichtyophis (PETER, 1898) a trois septa.

périlymphatique, le partage secondairement en deux. La bande de tissu s'ossifie immédiatement. Ce mode de formation du trou périlymphatique est à bien distinguer de celui des deux trous périlymphatiques des Anoures. Car chez *Hynobius* on trouve un trou divisé secondairement qu'on peut comparer avant sa subdivision au trou périlymphatique supérieur des Anoures.

La formation du trou périlymphatique inférieur des Anoures est en rapport étroit avec le développement considérable de la pars basilaris et de la lagena et avec le plus haut degré de développement du système périlymphatique dans ce groupe. HARRISON (1902) qui a fait une étude spéciale du développement du système périlymphatique des Amphibiens, croit que ce trou apparaît chez les Anoures sous l'influence du recessus partis basilaris et indépendamment du trou périlymphatique supérieur.

L'histoire du développement d'*Alytes* nous a montré qu'il n'est pas permis de considérer ces deux orifices comme un « foramen rotundum » (HASSE, 1872) subdivisé. PEETERS aussi considère les deux orifices de *Rana* comme préformés.

En faveur de l'hypothèse de HARRISON, mes recherches m'ont fait voir qu'il n'est pas exact que deux orifices périlymphatiques se forment chez tous les Anoures. Cela est vrai pour les Anoures phanéroglosses adultes (quelquefois on trouve chez la larve un seul orifice; *Bufo*, selon HARRISON), mais non pour *Pipa americana*, où il n'y a que le trou interne. Le système périlymphatique de cette espèce est très peu différentié, encore moins que celui des Urodèles. Un recessus partis basilaris, qu'on trouve chez *Triton*, *Salamandra* (HARRISON) et *Hynobius* (OKAJIMA) comme une petite saillie du canal périlymphatique, manque tout à fait ici (1). La pars basilaris se joint directement au canal périlymphatique. Celui-ci entre dans la cavité crânienne par le trou

(1) Il est possible qu'un petit recessus se développera encore chez l'animal adulte ; la disposition décrite ci-dessus se trouve dans des larves en métamorphose (longueur du corps : 11 ½ mm., de la queue : 12 ½ mm.

périlymphatique interne, situé dans la cloison capsulaire médiale, se recourbe en direction caudale et finit en cul-de-sac dans le spatium meningeale qui s'étend jusqu'au trou jugulaire.

En général, on peut dire qu'on trouve un seul orifice périlymphatique situé dans la cloison capsulaire médiale, si le recessus partis basilaris est absent (*Pipa*) ou peu développé (les Urodèles ; *Hynobius*, au stade larvaire) et s'il est placé en dedans de la capsule auditive. Ce trou est évidemment phylogénétiquement le plus ancien.

On trouve pour la première fois le trou périlymphatique inférieur (externe) chez les Anoures phanéroglosses qui ont le recessus partis basilaris bien développé. D'après les données acquises sur le développement et la situation des deux orifices, périlymphatiques, il est clair que les noms proposés par Peeters (1910) : interne et externe sont préférables à ceux de Gaupp : supérieur et inférieur.

L'existence d'un trou périlymphatique accessoire chez *Rana* n'est pas absolument certaine. Gaupp et Harrison l'affirment, mais Peeters ne l'a pas observé ; peut-être est-ce parce que la cloison cartilagineuse, qui sépare chez *Rana* le trou accessoire du trou jugulaire existe depuis trop peu de temps. On peut aussi supposer que la formation de cette cloison, tout comme celle entre les trous acoustiques antérieur et postérieur est quelquefois absente.

Gaupp (1911) mentionne en passant [1] que quelques Anoures, comme *Alytes* et *Bombinator*, ont un canal facial, mais il ne donne aucun renseignement sur son développement. Il l'ignorait encore lorsqu'il essaya, dans son ouvrage de 1893, d'expliquer le parcours différent du nerf facial chez les Urodèles et les Anoures. Gaupp prit comme point de départ commun le trajet du facial chez *Siredon*, *Necturus* et *Amphiuma*, dont il dériva d'une part la disposition chez *Triton*, d'autre part celle de *Rana*. Selon lui, le nerf facial chez *Siredon* n'entre dans la capsule auditive qu'en apparence ; en

[1] Chez *Pipa* et *Xenopus* il n'y a pas de trou ou de canal du N. VII.

réalité, il parcourt un canal cartilagineux, situé au côté ventral de la cupule antérieure. La voûte de ce canal est formée par cette cupule et son fond par le plan basal. Si le toit manque, on a la disposition de *Triton* (1) ; si c'est le fond — et par conséquent la jonction entre le plan basal et la capsule auditive — on a le cas de *Rana* et des autres Anoures.

Le développement du canal facial chez *Alytes* me fait douter de cette opinion, parce que j'ai vu que la plus grande différence entre *Rana* et *Alytes* n'est pas la formation du canal, mais bien le fait que le nerf facial entre réellement dans la cavité de la capsule auditive et longe le côté *latéral* de la cloison médiale de cette capsule. Chez *Rana* et la plupart des Anoures, le trajet *médial* est normal. *Alytes* montre en même temps comment on pourrait conclure de l'isolement postérieur du N. VII dans le canal cartilagineux, que le nerf facial ne pénètre pas dans la capsule auditive et qu'il est situé entre la capsule auditive et le plan basal ; ce serait inexact.

Les recherches de PEETERS (1910) montrent qu'il ne se forme pas de canal chez *Siredon* et *Necturus* et que le canal de *Triton* se forme par la croissance d'un rebord de la capsule auditive, saillant en dedans. PEETERS a suffisamment démontré que la théorie de GAUPP au sujet des Urodèles n'est plus soutenable.

Le trajet du nerf facial d'*Alytes* en dedans de la capsule auditive et du côté latéral de la cloison médiale de cette capsule et son enveloppement secondaire dans un canal, donne à *Alytes* et probablement aussi à *Bombinator* (2), une position particulière parmi les Anoures examinés jusqu'à présent. Par rapport à la disposition chez les Urodèles on peut considérer cela comme un état primitif.

Parmi les Poissons, Reptiles, Oiseaux et Mammifères,

(1) Contrairement à l'observation de GAUPP, MISS PLATT et PEETERS ont démontré que le nerf facial entre chez Triton dans la capsule auditive.

(2) GÖTTE (1875) ne mentionne pas un tel parcours du nerf facial chez *Bombinator* ; ses figures ne l'indiquent pas non plus.

on trouve souvent des orifices spéciaux pour le nerf facial et en certains cas (chez quelques Sélaciens, Oiseaux et Mammifères) un canal facial (GAUPP, 1911 en donne un résumé), mais toujours il s'agit d'un trajet extracapsulaire du N. VII. Chez *Petromyzon* le facial et l'acoustique entrent ensemble dans la capsule auditive ; le premier quitte cette capsule par un trou de son plancher (KETEL, 1873).

La fenêtre ovale primaire se ferme de la même façon chez *Alytes* que chez *Rana* (GAUPP, 1893) et se transforme en fenêtre ovale secondaire. Chez *Rana* elle se rétrécit en direction cranio-caudale. Sa limite caudale reste à peu près la même. De même l'orifice diminue, parce que le cartilage de la cloison capsulaire ventrale croît en direction latérale.

Les opinions des auteurs sur l'origine du tectum posterius (synoticum) diffèrent. Quelques-uns le considèrent comme une partie de l'arc occipital, tandis que d'autres lui attribuent une certaine indépendance ou le dérivent de la capsule auditive.

PARKER et GOETTE adoptent la première opinion, WIEDERSHEIM et STÖHR la seconde. Dans la littérature ultérieure, cette opposition persiste.

Quant aux Anoures, on trouve seulement chez GAUPP et PEETERS des renseignements sur *Rana*.

GAUPP (1893) observa dans une larve de 16 mm. le rudiment du tectum posterius. Celui-ci est déjà tout à fait développé dans une larve de 21 mm. Une pièce médiane indépendante, unie par du tissu fibreux aux bords de la capsule auditive, se forme d'abord. Selon GAUPP le tectum ne provient pas de la croissance et de l'union médiane de ces bords, mais d'une chondrification indépendante de la voûte crânienne. Dans une larve de *Triton* de 12 mm. il trouva une formation analogue.

PEETERS (1910) a une autre opinion. Chez *Rana* il n'a jamais vu la formation indépendante du tectum posterius. Il considère ce tectum comme une partie de l'arc occipital, qui se joint à la capsule auditive au moment où celle-ci s'est déjà chondrifiée en partie. Pour cette raison chez *Rana* le

tectum posterius a l'air de croître à partir de la capsule auditive, tandis qu'il appartient en réalité à l'arc occipital.

A cet égard les données chez les Urodèles permettent en général l'interprétation que le tectum posterius fait partie de l'arc occipital. MISS PLATT (1897) observa chez *Necturus* que deux pièces cartilagineuses apparaissent indépendamment (¹) et elle les compare aux pièces qui unissent les extrémités dorsales des arcs neuraux. L'arc occipital s'unit d'abord à la capsule auditive, puis au tectum interoccipitale (²). WINSLOW (1898) qui considère aussi le tectum comme un prolongement de l'arc occipital, ne vit, ni chez les Urodèles, ni chez les Anoures, de centre cartilagineux indépendant, probablement faute de stades convenables. PEETERS (1910) chez *Triton*, ne put observer la formation du tectum posterius, mais quelques préparations in toto lui firent conclure que le tectum ne se forme pas indépendamment. Il se développe en étroit rapport avec l'arc occipital qui se prolonge en direction rostrale et latérale sur la cloison de la capsule auditive, jusqu'à l'endroit où plus tard le tectum apparaîtra. Chez *Necturus* le tectum est un prolongement de l'arc occipital qui se recourbe en direction rostrale et médiale et s'unit à la capsule auditive. C'est à cause de ces observations que PEETERS considère le tectum posterius comme une partie de l'arc occipital. Son argument principal est tiré de la forme définitive du tectum (lequel est un prolongement de l'arc occipital et de la crête occipitale latérale) et du mode d'ossification qui ressemble fort à celui d'un véritable arc vertébral. Mais la différence entre la fermeture de l'arc occipital et celle de l'arc vertébral, telle que PEETERS et d'autres l'ont observée, est toujours celle-ci : l'union cartilagineuse, médiale du premier se dirige en direction rostrale, l'union du second en direction caudale.

(¹) WINSLOW (1898) ne les a pas trouvées et PEETERS (1910) doute de leur existence.

(²) Sur la proposition de GAUPP, MISS PLATT a changé le nom : tectum synoticum en tectum interoccipitale, quoique GAUPP lui-même croie que l'unité génétique du tectum et de l'arc occipital n'est pas démontrée.

Gaupp (1906) proposa, en attendant que l'origine du tectum soit élucidée, le nom de « tectum posterius » au lieu de « tectum synoticum », parce que dans ce nom, ni la connexion avec les capsules auditives, ni celle avec l'arc occipital ne sont exprimées.

Il me semble probable que le tectum posterius des Amphibiens et autres a une origine *double* et qu'on pourrait y distinguer une partie occipitale, ayant le caractère d'une vertèbre et une partie de la voûte qui se prolonge en taenia tecti medialis, ou qui après son developpement total forme la voûte cranienne. Parfois le composant occipital est bien marqué (les Urodèles), ce que l'on peut attribuer à la réduction très marquée de la voûte cranienne. L'arc occipital des Urodèles a mieux conservé son caractère de vertèbre que l'arc homonyme des Anoures qui, comme je l'ai démontré plus haut, correspond à l'arc préoccipital des Urodèles. La situation caudale et libre de l'arc occipital chez *Necturus* est la cause que la partie dorsale de l'arc neural peut se manifester et qu'un véritable *tectum interoccipitale* se forme (cf. Peeters, 1910 ; fig. 3, pl. 1). Cette partie dorsale de l'arc occipital ne se développe pas chez les Anoures d'après ce que j'ai pu observer chez *Alytes*. Si elle se développait véritablement, *Alytes* le montrerait sans doute, car l'arc occipital y est très précoce. Le centre cartilagineux dorsal (larve de 7 mm.) se trouve, à la partie caudale de la paroi capsulaire médio-ventrale, à l'endroit où plus tard se trouvera la crête occipitale latérale. Le tectum posterius se développera plus tard (larve de 12 ½ mm.) et se trouvera alors assez loin rostralement, précisément derrière le canal endolymphatique.

Il me semble qu'il est impossible d'admettre dans ce cas un rapport direct entre l'arc occipital et le tectum posterius. Aussi je suis d'avis qu'il y a chez *Alytes* et chez les autres Anoures un véritable tectum synoticum, c'est-à-dire une partie de la voûte cranienne qui relie les capsules auditives et se développe de bonne heure.

Si cette interprétation est exacte, le composant de l'arc

occipital manquerait dans le tectum posterius des Anoures, tandis que chez les Urodèles le composant de la voûte serait fortement réduit.

La largeur du tectum chez *Alytes* s'accorde avec les données de GAUPP sur *Rana* où le bord postérieur se trouve dans le plan du trou périlymphatique supérieur et le bord antérieur dans celui du trou endolymphatique. Mais chez *Alytes* il n'y a pas de déplacement caudal du cerveau pendant le développement. A tous les stades le bord antérieur du tectum et l'origine du N. VIII sont situés dans le même plan. Chez *Rana* le cerveau se déplace de telle manière que le bord antérieur, qui est situé d'abord au-dessus de la moelle allongée, finit par être placé au-dessus des parties caudales du mésencéphale.

L'absence d'une taenia tecti medialis semble ne pas être primitive, mais doit être due à une rédnction, parce qu'on peut admettre que la voûte cranienne était originellement tout à fait cartilagineuse comme chez les Sélaciens. Il y a nombre d'Anoures qui possèdent, comme *Rana*, deux fontanelles postérieures, mais on en trouve aussi plusieurs qui montrent une voûte cranienne fermée (cf. les figures de PARKER, 1881). Chez *Triton* la réduction est apparemment plus avancée que chez *Amblystoma*, où WINSLOW (1898) observa chez une larve de 39 mm. une courte saillie médiale.

Une seule fontanelle postérieure, bien développée, ne se trouve parmi les Anoures que chez *Alytes* et il est à remarquer que chez l'adulte les fronto-parietalia étroits qui s'unissent seulement dans leurs parties caudales au-dessus du tectum posterius, couvrent la cavité cranienne très insuffisamment, de sorte que les fontanelles antérieures et postérieures, séparées par la taenia tecti transversalis, sont tout à fait à découvert.

Le développement des crêtes marginales se fait, tout comme celui des taeniae tecti marginales chez *Rana*, en direction rostrale à partir du tectum posterius. Chez *Triton* il n'y a pas de taeniae ou de crêtes.

La crista parotica de *Rana* est située au côté rostro-

latéral de la capsule auditive. Elle s'unit avec l'apophyse ascendante. PEETERS a signalé avec raison que l'absence du « processus oticus » chez *Alytes* nous fait comprendre que la crista parotica tire son origine uniquement de la capsule auditive.

C. Operculum et Plectrum

Stade II

La fenêtre ovale est limitée du côté dorsal par le bord ventro-médial du cartilage environnant le canal demi-circulaire latéral, et du côté ventral par le fond horizontal de la capsule auditive qui est à peu près plat. On trouve dans la fenêtre : l'operculum, la pars interna plectri et un tissu remplissant l'orifice qui se colore, dans des stades plus avancés, par le bleu de Lyon, en bleu foncé.

La forme de l'operculum est une ellipse courte, conchyforme et un peu effilée en avant ; sa longueur est tout au plus de 0.8 mm., sa hauteur 0.7 mm. L'operculum s'étend jusqu'à 0.3 mm. du bord antérieur de la fenêtre et recouvre le reste de cet orifice, en se serrant contre son bord supérieur. Au côté caudal l'operculum se continue en s'épaississant vers le bord postérieur de la fenêtre, là où le muscle operculaire s'attachera plus tard. Cet épaississement est accolé contre la paroi de la capsule auditive et en est séparé par une bande de tissu connectif très mince. Au côté ventral, entre l'operculum et le bord de la fenêtre, il y a une fente, qui est remplie par le tissu de la fenêtre, lequel possède de nombreuses fibres élastiques. Ce tissu existe aussi autour et en avant de la pointe de l'operculum.

Dans le coin supérieur rostral de la fenêtre on trouve la pars interna plectri qui à ce stade est déjà cartilagineuse en partie. Ce cartilage se prolonge un peu devant la fenêtre par une bande de noyaux très serrés, visible jusqu'au-dessous du palatocarré et disparaît dans le tissu environnant, un peu devant l'apophyse ascendante, uu côté médial du N. hyo-

mandibulaire et entre le muscle ptérygoïdien et le muscle dépresseur postérieur de la mandibule. Le cartilage de la pars interna plectri est situé à l'intérieur de la fenêtre et contre le tissu qui la remplit.

Le trajet du N. IX, de la veine jugulaire et de l'artère carotide est le même que chez les larves de *Rana fusca* de ce même stade.

Développement

La chondrification de l'operculum débute chez une larve de 22 mm. dans le coin inférieur, caudal de la fenêtre ovale ; dans une larve de 16 mm. le rudiment de l'operculum est représenté par une accumulation de noyaux dans le tissu de la fenêtre. Le premier développement du cartilage a donc lieu à des stades intermédiaires.

Au stade de 16 mm. le bord ventral de la fenêtre ovale n'est pas limité distinctement par du cartilage et on peut observer qu'il se transforme petit à petit dans le tissu recouvrant l'orifice de la fenêtre, lequel s'amincit vers le haut et se termine dans le périchondre du cartilage entourant le canal latéral, en s'amincissant fortement.

Dans une larve de 22 mm. la limite ventrale de la fenêtre est nette à sa partie caudale, mais à sa partie rostrale elle l'est moins. Le cartilage de l'operculum, sur une coupe transversale, a la même épaisseur que la bande étroite du tissu à noyaux nombreux qui l'unit au bord ventral de la fenêtre. Le tissu qui remplit l'espace entre l'operculum et le bord supérieur de la fenêtre, est au contraire très mince. Donc, il est évident qu'on peut considérer le tissu à noyaux denses comme un prolongement de la paroi capsulaire ventrale et l'operculum comme une pièce de cartilage en provenant.

Dans une larve de 25 mm. l'operculum s'est étendu en direction caudale au delà du bord postérieur de la fenêtre. La pars interna plectri de ce stade est encore visible comme une accumulation de noyaux, situés contre le tissu qui remplit le coin supérieur rostral de la fenêtre.

Littérature

GAUPP (1893) a observé que l'operculum cartilagineux apparaît dans une larve de *Rana fusca* de 29 mm., comme une formation indépendante dans le tissu qui remplit la fenêtre ovale. Le plectrum se forme pendant la métamorphose. La chondrification de la pars interna plectri commence dans une larve de 29 mm. et on peut la suivre dans le « ligamentum suspensorio-columellare » jusqu'au dessous du palatocarré. Cela se passe dans le tissu qui remplit le coin supérieur rostral de la fenêtre. Le bord ventral de l'operculum est, dès le début, séparé du bord inférieur de la fenêtre par une fente assez large.

Conformément à mes propres observations, PEETERS vit chez *Alytes* dans une larve de 25 mm. la formation indépendante de l'operculum tout près du bord caudal et ventral de la fenêtre.

KOTHE (1910) a trouvé chez une larve de *Pelobates* de 37 mm. dans la fenêtre ovale secondaire, un mince operculum cartilagineux dont il ne put observer le développement; c'est dans une larve de 75 mm. qu'il a vu la première formation du plectrum dans cette partie rostrale de la fenêtre ovale que l'operculum ne couvre pas.

On peut dire en général que chez les Anoures l'operculum se forme le *premier* et longtemps avant la métamorphose, tandis que le plectrum (pars interna plectri) se chondrifie *plus tard*, juste avant la métamorphose et atteint son développement complet dans l'animal adulte. Cette règle est de rigueur seulement pour les Anoures *phanéroglosses*. Chez les Anoures *aglosses* il n'y a probablement pas de formation particulière de l'operculum. Le premier cartilage dans la fenêtre ovale apparaît, comme j'ai pu l'observer chez une larve de *Xenopus*, au même moment que celui où le plectrum pourrait se former. Chez une larve de *Pipa* en métamorphose le cartilage auditif est aussi peu développé et il n'y a pas d'operculum indépendant. Il est fort important de constater chez les deux espèces que le cartilage ne se montre pas dans la partie

caudale du tissu qui remplit la fenêtre, mais seulement dans la partie rostrale, tout comme s'il s'agissait de la formation du plectrum (1). Faute de matériel suffisant il est impossible de dire avec certitude, si cette pièce cartilagineuse représente une columelle, telle que l'on peut en trouver chez quelques Urodèles (*Necturus*, *Proteus*). Chez *Necturus* par exemple, on trouve selon REED (1913) une columelle (operculum, MISS PLATT, 1897 ; PEETERS 1910), qui apparaît de bonne heure et qui est d'origine extra-otique. Des éléments du tissu du bord caudal de la fenêtre se joignent plus tard à cette columelle ; ils représentent la pars opercularis. Un tel mode de formation de la columelle pourrait se présenter aussi chez les Aglosses.

Il est certain, d'après KINGSBURY et REED (1909), que l'operculum est d'origine labyrinthique et n'a pas de rapport avec l'arc hyodien, contrairement à la columelle (pars interna plectri des Anoures phanéroglosses), qui est d'origine extra-otique et qui appartient très probablement à l'arc hyoïdien. Par plusieurs arguments KINGSBURY et REED (1909) ont rendu admissible l'homologie hyomandibulaire de la columelle et MARCUS (1910) a pu prouver chez *Hypogeophys* (Apodes) l'unité de l'ébauche de la columella et de cellede l'hyoide.

Un mode de formation de l'operculum fréquent chez les Urodèles, est le découpage par histolyse d'une partie de la cloison capsulaire ventrale, peu avant ou pendant la métamorphose (*Amblystoma, Chondrotus tenebrosus* : KINGSBURY et REED, 1909, *Triton* : FUCHS, 1907.)

Chez quelques Urodèles, KINGSBURY et REED (1909) ont trouvé d'autres modes de formation des cartilages auditifs. Deux d'entre eux nous arrêteront. Chez les Plethodontidae et les Desmognathidae, le cartilage auditif a pris à la fois

(1) Chez une larve de *Xenopus* (sans pattes antérieures, les 3/7 de la fenêtre ovale restent à découvert. J'ai observé la même disposition chez une larve de *Pipa* en métamorphose (longueur totale 20 mm., la queue encore visible, les pattes antérieures et postérieures bien développées). La partie proximale du plectrum en ces deux cas est épaissie et se joint au tissu remplissant la fenêtre. Il est possible que cette partie proximale représente une pars opercularis.

le caractère de columelle et d'operculum, et dans l'ontogénie il est impossible de montrer qu'ils sont séparés (*Spelerpes bilineatus*). Par l'agrandissement de la plaque cartilagineuse, la fenêtre ovale se ferme. Il y a pourtant selon KINGSBURY et REED deux raisons de distinguer une pars opercularis de la columelle dans ces deux familles : 1° on trouve à cette partie une prominentia perilymphatica, dans laquelle est situé le recessus perilymphaticus (qui se trouvent d'habitude à l'operculum et en dedans de lui) ; 2° un muscle operculaire s'attache à cette prominentia. J'ai constaté que ces deux criteria manquent chez *Pipa* (1). Il sera donc très difficile de prouver l'existence d'une pars opercularis chez les Aglossa. Surtout parce que, à mon avis, il est peu probable qu'on trouve chez *Pipa* et *Xenopus* (2) une formation particulière de l'operculum et une union des éléments du bord caudal de la fenêtre au plectrum.

Outre la comparaison avec le mode de développement chez les Plethodontidae et les Desmognathidae, il reste encore une deuxième possibilité. On peut comparer la disposition chez les Aglossa avec celle de *Cryptobranchus alleghaniensis* et de *Megalobatrachus*. Chez eux, au stade larvaire, on ne peut pas reconnaître d'operculum à part et selon KINGSBURY et REED les criteria indiqués ci-dessus font défaut également.

Il n'est pas nécessaire d'attribuer la présence d'une columella sans pars opercularis à la réduction de l'operculum et du muscle operculaire. On a de bonnes raisons pour considérer cette disposition comme primitive. En ce cas, phylogéniquement, l'operculum serait apparu plus tard que la columelle.

Les considérations suivantes peuvent étayer cette supposition : 1° COPE (1888) a trouvé chez quelques Stégocéphales du Permien (*Trimerorhachis Cope* et *Zatrachys Cope*), appar-

(1) Certains renseignements disent que *Xenopus* ne montre pas de formation particulière du plectrum. Dans la partie rostrale de la fenêtre ovale de ma larve de *Xenopus* avant la métamorphose, j'ai trouvé seulement une pièce de cartilage et pas d'operculum particulier.

(2) KINGSBURY et REED (1909) font de même cette comparaison.

tenant aux Temnospondyli, que la fenêtre ovale est fermée par une columella auris non segmentée. Celle-ci conduit à une solution de continuité, délimitée par le squamosum, le supratemporale et le tabulare, et dans laquelle une espèce de myringe du tympan aurait été tendue. Il n'y a pas d'operculum ; 2° L'operculum manque chez la larve de presque tous les Urodèles ; 3° On ne le trouve plus du tout chez *Cryptobranchus* et *Megalobatrachus* (en stade larvaire non plus) qui appartiennent aux Ichthyoidea, un groupe primitif des Urodèles.

L'origine de la columelle (pars interna plectri) ne sera pas examinée ici. Les Anoures ne donnent pas de bons arguments pour l'homologie hyomandibulaire, excepté le trajet du nerf facial. GAUPP (1906, p. 726) a dit : «Mit dem Hyale hat weder das Operculum noch das Plectrum ontogenetisch etwas zu thun ; dasselbe befindet sich beim Auftreten beider noch im vorderen Teil der Orbito-temporalregion in Verbindung mit dem Palatoquadratum ». Il est presque impossible de trouver l'adhérence de l'hyoïde avec la columelle chez les Anoures parce que l'hyoïde s'est déplacé trop loin en avant.

La disposition chez les Anoures phanéroglosses, à cet égard, nous fait conclure tout au plus à l'origine extra-otique de la pars interna plectri et rien de plus. Les stades importants des Aglosses, qui peut être donneraient des renseignements, me manquent.

Après les recherches de KINGSBURY et REED et de MARCUS, l'origine hyale de la columelle des Urodèles et des Gymnophiones me semble admissible.

D. Regio orbitalis

Stade II

La fontanelle de la base, sur laquelle se trouve l'hypophyse, est fermée presque entièrement ; le reste de la base crânienne est cartilagineuse. Au-dessous de l'hypophyse le

cartilage est très mince (une seule couche de cellules) ; mais en direction crâniale son épaisseur augmente, et il se transforme successivement en cartilage du plan internasal. Deux orifices persistent des deux côtés de la base du crâne : le trou carotidien et le trou cranio-palatin.

La paroi latérale est entièrement cartilagineuse et unie par une arche cartilagineuse à la capsule auditive, de sorte que le trou prootique est entouré par du cartilage. Le trou de l'oculomoteur que traversent le N. oculomoteur et l'artère ophtalmique, se trouve en partie au-dessous de l'apophyse ascendante et juste au-dessus du trabécule primitif ; il est devenu relativement beaucoup plus petit, si on le compare aux stades plus jeunes.

La limite crâniale du trou oculomoteur est formée par une mince cloison de cartilage, plus jeune que dans le reste de la paroi, à en juger par sa structure. Pour cela, cette paroi diffère fort en épaisseur du trabécule et de la partie centrale de la paroi latérale, qui se sont développés depuis longtemps. La paroi latérale est donc concave ; la concavité se trouve en dehors. Vis-à-vis du bord antérieur de la taenia tecti transversalis on trouve à droite le trou du N. IV, situé dans la partie dorso-latérale de la paroi juste au-dessous du fronto-parietal ; à gauche, l'orifice est plus caudal, en face du bord postérieur de la taenia. Le nerf optique croise le trabécule primitif, en passant par le coin caudal du trou optique et ne remplit qu'un tiers de l'orifice. A l'endroit où la paroi latérale se continue dans le trabécule, elle est toujours plus mince que celui-ci, mais devant le trou optique les deux se confondent.

La taenia tecti transversalis représente la voûte du crâne ; elle se forme probablement par la concrescence d'une pièce médiane avec deux pièces latérales, qui se sont développées à partir de la paroi latérale. Dans la série dont il est question, à droite, cette union vient de se faire ; à gauche, la concrescence est déjà complète. Le bord postérieur de la taenia est plat, le bord antérieur convexe.

La cavité cranienne est spacieuse par rapport au cerveau.

Développement

La formation de la base du crâne se fait peu après la formation du plan internasal ; j'ai trouvé ce dernier pour la première fois dans une larve de 12 ½ mm., où il réunit les trabécules, qui sont courbés en dedans.

La fenêtre basicrâniale antérieure de ce stade est fermée par du cartilage, à partir du plan internasal en direction caudale ; en même temps, la formation cartilagineuse continue à partir du côté médial des trabécules et en commençant juste derrièrele trou carotidien futur (larve de 16 mm.) On voit d'abord les trous de l'artère carotide et plus tard les trous cranio-palatins, puisque le cartilage qui entoure ces orifices se forme plus tôt que dans le reste de la base cranienne. Au début, le trou cranio-palatin est oblong (fig. 3 et 4, pl. VIII); plus tard il devient circulaire. Devant le plan trabéculaire le cartilage s'étend aussi, mais faiblement, parce que l'hypophyse met obstacle à la chondrification.

La base du crâne se chondrifie irrégulièrement et pas toujours de la même façon.

Au premier stade, la paroi latérale était encore en grande partie membraneuse et avait des orifices spacieux pour les N. II et N. III. Le cartilage se formait, comme je l'ai dit plus haut, en direction rostrale à partir du pilier de la paroi. On peut suivre à ce stade le cartilage du rebord de la paroi latérale jusqu'au delà du nerf optique, où il disparaît peu à peu dans la partie encore membraneuse. Chez une larve de 9 ½ mm., il existe du cartilage juste au devant de la commissure quadrato-craniale antérieure. Le cartilage du trabécule s'étire en longueur en coupe transversale et s'accroît vers le haut, à en juger par la superposition des cloisons cellulaires. Pourtant une partie de la paroi latérale presque chondrifiée reste placée entre le bord de la paroi et le cartilage développé en hauteur. Dans une larve de 12 ½ mm. leur réunion est parfaite et il n'est plus possible de distinguer les composants. Il me semble certain qu'en cet endroit, la chondrification progresse à partir du trabécule vers le haut.

Dans une larve de 9 ½ mm. les orifices des N. II et III ne sont pas encore limités de tous côtés par du cartilage. La cloison séparant les deux trous et la partie de la paroi devant le trou optique sont sur le point de se chondrifier. Une larve de 12 ½ mm. nous montre du cartilage à ces endroits. On ne peut pas observer avec certitude, si ce cartilage se développe à partir du trabécule où à partir du rebord de la paroi laterale, mais à en juger par les séries 13, 14 et 15, il semble que la chondrification parte des deux à la fois.

Le trou optique d'une larve de 25 mm. a le même diamètre en longueur que sur une larve de 53 mm. ; le trou oculomoteur au contraire devient plus étroit par l'accroissement en direction caudale de la cloison qui sépare les trous des N. III et II et prend ainsi ses dimensions définitives. Cette cloison de division dans une larve de 53 mm. suggère l'idée qu'elle est récente.

Le relèvement de la paroi latérale part du rebord latéral et est déjà fort avancé dans une larve de 22 mm. La paroi latérale se recourbe ensuite en direction axiale, de sorte que le cerveau est limité aussi à son côté dorso-latéral par du cartilage (fig. 3, pl. VIII).

En résumé, le développement de la paroi latérale tire son origine de deux centres principaux : le trabécule et le rebord de la paroi latérale. Tous deux se développent très tôt chez *Alytes* ; le trabécule naturellement le premier. Par le développement en direction rostrale de la paroi latérale qui commence à partir de son pilier, tôt formé, le cartilage du trabécule peut s'unir à ce rebord en face de la commissure quadrato-craniale antérieure. A peu près en même temps se chondrifient les parties de la paroi latérale interposées, encore membraneuses. Ainsi le trou du N. II et celui du N. III acquièrent une délimitation cartilagineuse définitive; le N. II d'abord, l'autre ensuite.

Dans une larve de 16 mm. le trou prootique a son pourtour dorsal formé par une arche cartilagineuse qui est un prolongement de cette partie de la paroi latérale, qui s'unit à la capsule auditive, en se recourbant en dedans.

Je n'ai pas pu constater de trou trochléaire, ni dans la paroi latérale encore membraneuse, ni à des stades plus développés (larve de 22 mm.). La ténuité de ce nerf en est peut-être la cause.

Dans ce stade de 22 mm. on voit un peu devant et au-dessus du trou optique un petit orifice, à travers lequel une branche mince de la veine jugulaire entre dans la cavité du crâne.

Du fait que le développement de la taenia tecti transversalis se montre dans des larves ayant une longueur de plus de 30 mm., je ne puis pas donner de renseignements à cet égard faute de séries et de préparations totales convenables.

Comme il a fallu enlever le cerveau du chondrocrâne dans la figure 3, pl. VIII, je ne puis pas affirmer, si la taenia de ce stade est cartilagineuse dans sa partie centrale. Pour la même cause les autres préparations totales que je possède, sont aussi sans valeur.

Littérature

Sur la fermeture cartilagineuse de la fenêtre basicraniale mes observations s'accordent avec celles de Peeters (1910) chez *Rana fusca* et *esculenta* et chez *Alytes*. Le trou carotidien est formé plus tôt que le trou cranio-palatin et la fermeture de la fontanelle hypophysaire est achevée ou à peu près avant la métamorphose, quoique le cartilage y soit très mince. Mes préparations totales de *Rana fusca* confirment ce point et donnent raison aux observations de Peeters, qui diffèrent à cet égard de celles de Gaupp sur *Rana fusca*. Peeters (1910, p. 129) traitant ces questions in extenso, je renvoie à son ouvrage.

Chez *Rana*, le développement de la paroi latérale tire, selon Gaupp et Peeters, son origine de deux points : du pilier de la paroi latérale vis-à-vis du processus ascendens et des environs de la commissure quadrato-craniale antérieure. Après que le N. III s'est entouré étroitement de cartilage, les deux saillies cartilagineuses s'unissent par un rebord dorsal cartilagineux (« dorsale Randspange »); la paroi

latérale s'étend comme une membrane dans la fenêtre, formée par le trabécule, la « dorsale Randspange » et les deux saillies. La chondrification de cette membrane se fait d'une part à partir du trabécule, de l'autre à partir de la « dorsale Randspange » ; le trou optique reste libre. Avant que ce rebord se soit formé, l'union du pilier de la paroi latérale avec la taenia tecti marginalis s'effectue et le trou prootique se trouve limité dorsalement par du cartilage.

Peeters (1910) a supposé que le développement de la paroi latérale chez *Alytes* serait différent de chez *Rana* et que les trabécules en seraient les points de départ. Quoique le développement de la paroi latérale d'*Alytes* diffère en quelques points de celui de *Rana*, on ne peut dire que la supposition de Peeters soit réalisée. Un développement de la paroi latérale à partir du trabécule ne peut être admis que pour la portion située en face de la commissure quadrato-craniale antérieure. Du reste, on trouve chez *Alytes* un rebord latéral, très tôt cartilagineux, à partir duquel le relèvement de la paroi latérale se produit. On ne peut parler ici d'une « dorsale Randspange » à cause de la situation *latérale* de ce rebord. *Alytes* nous montre aussi une fenêtre, quoiqu'elle soit moins distinctement limitée; la chondrification de la membrane se fait de la même manière que chez *Rana*.

Les différences entre *Rana* et *Alytes* sont les suivantes. L'enveloppement du N. III ne se fait pas immédiatement pendant le premier développement de la paroi latérale d'*Alytes*, mais le diamètre sagittal de l'orifice ne se rétrécit que beaucoup plus tard.

J'ai déjà signalé que la paroi latérale d'*Alytes* se chondrifie plus tôt que chez *Rana*, où la « dorsale Randspange » n'existe que dans une larve de 30 mm.

L'union de la paroi orbitotemporale avec la capsule auditive (limite dorsale du trou prootique) par du cartilage, nous montre chez *Alytes* une grande ressemblance avec les Urodèles, nommément *Triton* (Gaupp, 1906). Chez *Rana*, avec ses taeniae tecti marginales indépendantes, celles-ci passent dans la paroi latérale ; l'union directe avec les

capsules auditives se fait après la concrescence de celles-ci avec les taeniae. La réunion du pilier de la paroi latérale de *Rana* avec ataenia tecti marginalis se montre chronologiquement avant l'apparition de la « dorsale Randspange » ; au contraire, chez *Alytes* la paroi latérale se chondrifie d'abord (larve de 7 mm.) et la concrescence de la paroi latérale et de la capsule auditive vient ensuite (larve de 16 mm.).

La position du trou trochléaire qui m'a échappé jusqu'à des larves de 25 mm., s'accorde avec celle de *Rana* (c. f. Gaupp, 1893, fig. 24, pl. XIV). On voit sur cette figure, du côté dorsal et rostral du trou optique, un autre orifice que Gaupp ne décrit point ; Peeters aussi trouva parfois chez *Rana* deux orifices, dont l'un situé au-dessus du trou oculomoteur, l'autre au-dessus du trou optique. Il ne put déterminer lequel des deux donnait passage au N. IV. Dans une larve de 25 mm. d'*Alytes* j'ai observé que l'orifice caudal est traversé par le N. IV, tandis qu'une petite branche de la veine jugulaire entre dans le crâne par l'orifice rostral. Celui-ci se ferme plus tard ; au stade II à gauche se trouve un reste de l'orifice, plein de pigment, tandis que à droite il a déjà disparu.

Il est à remarquer que le N. trochléaire chez les larves plus âgées perfore non seulement la paroi latérale cartilagineuse, mais aussi le fronto-pariétal. Au stade II cela n'arrive pas encore, mais je l'ai observé sur une larve de 62 mm. et sur une de 55 mm. en métamorphose (chez cette dernière seulement à droite). Sans doute cela est en rapport avec l'extension latérale du fronto-pariétal qui s'étend parfois au delà de l'orifice du N. IV et est forcé de lui ménager un orifice.

Drüner (1900) a démontré pour *Salamandra maculosa* et pour *Triton taeniatus* (quelquefois) que le N. IV perfore le pariétal. Goghill (1902) a constaté le même fait pour *Amblystoma tigrinum* et Gaupp (1911) pour *Triton taeniatus, Spelerpes bilineatus* et *Desmognathus fuscus.* Chez *Triton* et d'autres le nerf passe tantôt par la suture entre le pariétal et l'orbitosphénoide, tantôt il perfore le pariétal.

GAUPP attribue la variabilité de ce parcours du N. IV chez les Urodèles au faible degré de développement du crâne primordial qui fait que de l'os secondaire se développe vigoureusement et coopère à la formation de la paroi latérale. C'est pour cela qu'il dit (p. 406) : « In dieser Hinsicht haben die Anuren ein primitiveres Verhalten bewahrt ; bei ihnen ist die primordiale Schädelseitenwand vollständiger, und so tritt dann bei ihnen (*Rana; Bombinator, Pelobates, Alytes*), der Trochlearis durch ein kleines, selbstständiges Foramen in dieser Schädelseitenwand, damit an das Verhalten bei Selachiern und Knorpelganoïden erinnernd ».

Alytes montre qu'à cet égard il n'y a pas de limite entre les Urodèles et les Anoures. Tandis qu'on trouve chez *Alytes* une paroi latérale bien développée avec un trou, il arrive parfois que le fronto-parietal est perforé.

Un trou indépendant dans la paroi latérale existe parfois aussi chez les Urodèles ; OSAWA (1902) le signale chez *Cryptobranchus japonicus*.

L'explication de l'origine du trou dans le pariétal, telle que GAUPP l'a donnée, n'est plus admissible. Car *Alytes* montre que le pariétal peut bien s'étendre en direction ventrolatérale, malgré la présence d'une paroi latérale cartilagineuse bien développée. Le faible degré de développement de celle-ci chez les Urodèles ne peut pas en être la seule cause. En outre, *Siredon* (GAUPP, 1911, p. 406, fig. 4) donne l'exemple net d'un pariétal s'étendant peu ou pas en direction ventrolatérale et qui est perforé par le N. IV.

On peut résumer ces données dans la formule générale suivante : le pariétal étend son bord latéral jusqu'à proximité du trou du N. IV. Ce trou peut se trouver dans une paroi membraneuse ou cartilagineuse ; or, quelle qu'en soit la cause, le pariétal semble avoir une tendance à s'étendre vers cet orifice, et il doit bien laisser un passage libre pour le nerf qui le traverse.

Donc il est normal que le trou trochléaire soit situé chez les Urodèles entre le pariétal et l'orbitosphénoïde et chez les Anoures juste au bord du fronto-pariétal. Comme variation

on trouve parfois parmi les Urodèles ou les Anoures, quelques spécimens ayant un pariétal percé. C'est la règle chez quelques Urodèles.

La supposition de PEETERS, que dans sa plus jeune larve d'*Alytes* (25 mm.) la taenia tecti transversalis cartilagineuse serait déjà formée, n'est pas confirmée par mes préparations. Dans une larve de 25 mm. on ne trouve aucune trace de cette taenia.

E. Regio ethmoïdalis, Suprarostralia

Stade II

Au voisinage de la commissure quadrato-craniale antérieure les N. olfactifs se détachent du télencéphale et se dirigent en avant à peu près parallèles, jusqu'à ce qu'ils atteignent les trous olfactifs, situés latéralement, juste derrière le plan praecérébral. A la hauteur de la commissure les parois latérales se sont recourbées assez fortement en dedans, et elles se réunissent plus rostralement encore dans le plan médian. Ainsi se forme la voûte et les nerfs olfactifs s'étendent alors dans une cavité bien délimitée et remplie de tissu muqueux, fermée à sa partie rostrale par le plan praecérébral. Ce plan, dans lequel on peut encore reconnaître la forme et la position des cornets trabéculaires, est devenu assez épais et limite la partie caudale du « cavum internasale ». Quatre parois dont l'origine est facile à retrouver par la forme et les dimensions des cellules cartilagineuses, délimitent ce cavum internasale, ovalaire à grand axe vertical. Les parois se forment par les cornes trabéculaires qui se relèvent, juste devant le plan praecérébral, par du cartilage développé plus tard sur leurs faces dorsales (1) ; puis s'abaissent et se continuent dans les cornets. Sur leurs côtés dorsaux ces cornets s'unissent par une mince bande de cartilage qui se prolonge jusqu'au point d'attache du ligament

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(1) Cf. pour un stade plus jeune fig. 9*a*.

quadrato-ethmoïdal. Cette bande cartilagineuse représente le revêtement dorsal du cavum, tandis que la paroi ventrale est formée par une bande de cartilage assez solide qui réunit les cornets à partir du plan internasal et se transforme en direction rostrale en ligament qui, après s'être divisé, s'attache aux deux extrémités des cornets.

Au point d'attache du ligament quadrato-ethmoïdal le cornet trabéculaire s'est élargi latéralement (processus lateralis, fig. 3, pl. VIII). L'union ventrale et cartilagineuse des cornets se termine juste devant ce processus et par conséquent les cornets sont alors complètement libres. Les bouts des cornets se recourbent presque rectangulairement en bas et là s'unissent par un ligament dorsal qui s'étend sur les saillies médiales des suprarostralia et les relie latéralement. Les suprarostralia s'attachent lâchement aux cornets trabéculaires par une bande étroite de tissu non cartilagineux coloré en bleu par le bleu de Lyon.

A mi-hauteur de la paroi latérale et de la face dorsale de la commissure quadrato-craniale antérieure, se trouve une saillie latérale qui se détache en un « processus antorbitalis ». Les muscles obliques supérieur et inférieur s'attachent au côté caudal de cette apophyse. Le rameau interne des narines (branche du rameau orbito-nasal ou ophtalmique V) se dirige en avant du côté dorsal de cette saillie de la paroi latérale et est bientôt enfermé avec l'artère homonyme dans un court canal. La paroi latérale forme le côté médial de ce canal, le processus antorbitalis le côté latéral ; à eux deux ils forment le côté ventral, tandis que le côté dorsal est représenté par une voûte encore membraneuse en grande partie (fig. 8).

A l'endroit où le processus antorbitalis s'écarte de la paroi latérale, fait saillie à droite une petite lame cartilagineuse qui s'unira avec la paroi latérale au-dessus du rameau interne des narines. A gauche au contraire cette union s'est déjà faite, mais le lien avec le processus antorbitalis est encore membraneux.

La voûte de la cavité nasale apparaît en forme de rebord cartilagineux dorso-latéral des deux côtés du plan praecé-

rébral et du cartilage unissant les faces supérieures des cornets.

Les parties du squelette nasal qui apparaissent à ce stade comme une accumulation de noyaux et qui se développent complètement pendant ou après la métamorphose, ne seront pas traitées ici.

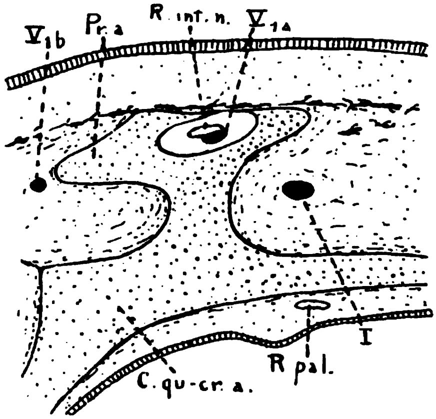

FIG. 8. — Coupe transversale d'une larve de 53 mm. (série 19) à travers la comm. quadrato-cr. ant. Gross. 30×.

Commencement de la formation du canal pour le R. internus narium V. Le toit est encore membraneux. La position de l'originelle paroi latérale est indiquée par un pointillage plus dense.

C. qu-cr. a., commissura quadrato-cranialis anterior ; *Pr. a.*, processus antorbitalis ; *R. int. n.*, ramus int. nar. de l'arteria orbitonasalis ; *R. pal.*, ramus palatinus de l'art. car. int. ; *I.*, nervus olfactorius ; *V1a* et *V1b*, ramus internus et externus narium V.

On peut distinguer aux *suprarostralia* une pièce médiane impaire qui limite l'orifice buccal au côté rostral, deux ailes bien développées et une paire de saillies dorsales, médiales qui s'articulent aux cornets trabéculaires (fig. 3 et 4, pl. VIII).

Les ailes s'élargissent latéralement en deux saillies, une dorso-latérale à laquelle s'attache le ligament mandibulo-suprarostral et une ventro-médiale sur laquelle deux muscles s'insèrent.

Directement derrière la pièce médiane se trouve un vaisseau sanguin dans le plan médian. Voici l'origine de cette artère, importante pour la comparaison des suprarostralia d'*Alytes* avec ceux des autres Anoures. Les rameaux palatins

des deux artères carotides internes qui parcourent en direction rostrale la cavité cranienne et la quittent par les trous cranio-palatins, se dirigent ensuite ventralement vers la base cranienne juste aux côtés médiaux des trabécules primitifs. Le rameau droit devient de plus en plus mince et se ramifie aux environs de l'orifice nasal externe en de nombreuses branches [1]. Le rameau gauche, gardant ses dimensions originelles, se déplace vers le plan médian, à l'endroit où le cartilage ventral, unissant les cornets, se transforme en ligament. Plus en avant, l'artère se trouve bientôt au-dessus de ce ligament et se recourbe enfin en direction ventrale, là où les cornets s'unissent aux suprarostralia. En suivant la ligne médiane des deux saillies dorsales, médiales, des suprarostralia, l'artère descend juste derrière le bord postérieur de la pièce médiane et se ramifie dans le tégument aux environs de la première rangée de dents palatines médiales.

Les rameaux internes des narines V, après avoir quitté le canal orbito-nasal et croisé le N. olfactif, suivent les surfaces dorso-latérales des cornets trabéculaires, se courbent en direction ventrale, en suivant les extrémités des cornets et les saillies médiales des suprarostralia et finissent par se ramifier dans le tégument.

Développement

Au premier stade, la position du cerveau à l'égard des cornets trabéculaires est telle que le bord antérieur du télencéphale dépasse le bout des cornets. Les fibres nerveuses du N. olfactif passent directement dans l'epithelium olfactif. Les cornets supportent donc une partie du télencéphale. Dans une larve de 12 ½ mm. le bord antérieur du cerveau dépasse le plan internasal, développé depuis peu. Au cours du développement on voit pousser les cornets en direction orale. Ils sont à peu près parallèles.

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[1] Cf. les figures 9 et 12 pour des stades plus jeunes.

La limite rostrale de la fenêtre basicraniale antérieure se forme par le développement du plan internasal entre les parties des trabécules les plus recourbées l'une vers l'autre. Le rudiment de ce plan est déjà présent dans une larve de 9 ½ mm. et il est chondrifié dans une larve de 12 ½ mm. Il se prolonge en direction orale (larve de 16 mm.) dans la bande cartilagineuse qui unit les cornets à leur côté ventral.

Les cornets trabéculaires et le plan internasal forment la base du plan praecérébral futur. Le rudiment cartilagineux de ce plan devient visible dans une larve de 16 mm. comme une élevure, située entre les cornets au dessus du plan internasal, laquelle dépasse les cornets en avant, à gauche et à droite (fig. 9, *c*, *b*, *a*). La chondrification procède d'après la

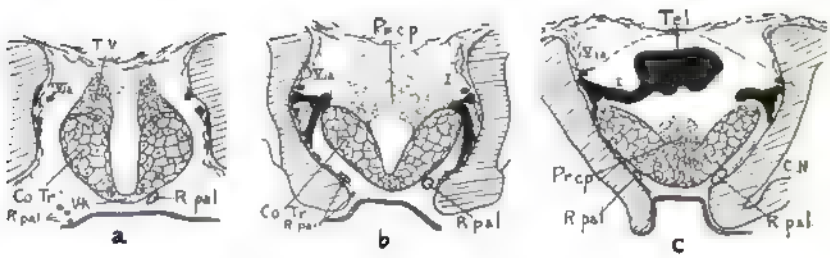

FIG. 9 *a-c*. — Coupes transversales d'une larve de 16 mm. (série 15) ; *a* se trouve à la partie la plus rostrale. Gross. 45×.

Rudiment du plan cérébral ; dans la figure b le cartilage n'est développé que très faiblement; l'organe olfactif est haché.

C. N., cavum nasi ; *Co. Tr.*, cornu trabeculae ; *Prc. p.*, plan précérébral ; *R. pal.*, ramus palatinus de l'arteria carotis interna ; *T. V.*, saillie de la trabécule ; *Tel.*, telencephalon ; *V. K.*, cartilage, unissant les côtés ventraux des cornets ; *I.*, nervus olfactorius ; *V1a*, ramus internus narium V.

couleur et les dimensions des cellules à partir du plan internasal et des saillies cartilagineuses, situées en avant des N. olfactifs, à la face supérieure des cornets trabéculaires. En raison de ce mode de formation, on pourrait admettre un composant du plan internasal et des composants des cornets qui formeraient par leur union le plan praecérébral. Au stade prochondral (12 ½ mm.) il n'y a pas de fenêtre ethmoïdale.

Les saillies sur les cornets (fig. 9 : TV) croissent par-dessus les N. olfactifs en direction caudale et s'unissent à la paroi latérale ; les trous olfactifs sont complets dans une larve de 22 mm.

Le rudiment du processus antorbitalis se montre à ce même stade larvaire.

La partie médiane des suprarostralia n'est pas encore cartilagineuse dans une larve de 12 ½ mm., mais les ailes et les saillies médianes le sont. Dans une larve de 16 mm. la pièce médiane cartilagineuse est très mince et sans suture.

Littérature

Le plan internasal de *Rana* est plus précoce que celui d'*Alytes*. Chez *Rana* (Stöhr, 1882), la chondrification des trabécules semble coïncider avec leur réunion. Dans une larve de 7.5 mm. (Stöhr, fig. 18, Taf. III), la juxtaposition est déjà faite. Dans une préparation totale de *Rana fusca* j'ai vu les trabécules s'unir et le plan internasal se former avant la formation du plan trabéculaire impair. Chez *Alytes*, au contraire, ce plan se forme plus tôt que l'internasal. Selon une figure de Goette (1875, Taf. XVIII, fig. 324), *Bombinator* se comporte comme *Rana*.

Born (1876) a observé que le plan précérébral procède chez *Pelobates* du développement de deux piliers qu'il nomme « Produkte der Trabekel ». Ils entourent une fenêtre qui est d'abord remplie de tissu muqueux et se chondrifie plus tard.

Gaupp (1893) a constaté le même fait chez *Rana fusca*, où le plan praecérébral se constitue de trois composants : les deux piliers ethmoïdaux (larve de 21 mm.) qui se dressent sur le plan internasal et une pièce médiane qui provient de la chondrification du tissu muqueux dans cette fenêtre ; chez une larve de 31 mm. celle-ci s'est fermée.

Peeters (1910) a confirmé et précisé les données de Gaupp concernant *Rana fusca*.

Rana esculenta diffère de *Pelobates* et de *Rana fusca*, comme Born l'a montré et Peeters l'a confirmé, par la formation

du plan praecérébral. La fenêtre praecérébrale fait défaut et il se forme d'abord une saillie cartilagineuse sur le plan internasal.

A ces deux points de vue il me semble qu'*Alytes* se rapproche plutôt de *Rana esculenta* que de *Rana fusca.*

Chez les Urodèles la fenêtre praecérébrale ne se ferme pas.

Le rudiment du planum antorbitale (1) apparaît chez *Rana fusca* et *esculenta* dans le coin situé entre la commissure quadrato-craniale antérieure et la paroi latérale. Chez *Alytes* ce point est situé plus dorsalement à mi-hauteur de la paroi latérale.

Chez *Rana*, le rameau interne des narines ne passe pas dans un canal ; il y a un trou orbito-nasal que le N. orbito-nasal V traverse en se rendant de l'orbite à la cavité nasale.

Je n'ai pas pu trouver dans des préparations totales de *Rana fusca* les apophyses latérales des cornets, unis par des ligaments aux apophyses quadrato-etmoïdales. Gaupp ne les dessine pas non plus dans ses reconstructions. Chez *Rana esculenta*, il existe d'après la figure de Peeters (pl. I, fig. 6), de semblables saillies aux cornets et selon les figures de Parker elles sont surtout bien développées chez *Pseudis paradoxa, Calyptocephalus gayi, Cycloramphus culeus, Hyla spec.* et *Bufo chilensis.*

Avec raison Peeters a comparé le cartilage qui unit les côtés ventraux des cornets, au ligament intertrabéculaire inférieur de *Rana*. La présence d'un ligament intertrabéculaire supérieur chez *Rana* est douteuse. Gaupp (1893, p. 417) dit que ce ligament : « aber weniger ein dichterer Strang, wie das Ligamentum intertrabeculare inferius, als vielmehr ein Pigmentzellen-Zug ist. » A mon avis, ce n'est pas un ligament. Il est vrai qu'on trouve chez *Alytes* un ligament dorsal qui relie les bouts *distaux* des cornets, mais *pas* dans la région des cavités nasales.

Quand on regarde de face les suprarostralia de *Rana*

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(1) Le nom « processus antorbitalis » est plus conforme à la réalité dans les plus jeunes stades avant la métamorphose.

fusca, on remarque, selon PEETERS, deux orifices par lesquels deux vaisseaux sanguins passent [1]. Dans les préparations totales ces ouvertures sont très nettes ; dans les coupes elles ne sont pas si clairement visibles. C'est probablement pourquoi GAUPP ne les décrit pas [2]. Dans les trois séries de *Rana fusca* que j'ai pu examiner, je les ai trouvées seulement à droite ; PEETERS a fait la même observation.

Chez *Rana esculenta* on peut encore trouver selon PEETERS, deux fenêtres latérales, fermées par une membrane et une ouverture médiale, qui est apparemment un reste de la grande fente, qui chez *Rana fusca* divise les deux suprarostralia (PEETERS, 1910, pl. I, fig. 11). Selon PEETERS (p. 154), ces fenêtres latérales non fermées et les trous pour les vaisseaux sanguins sont les restes de subdivisions disparues pendant la phylogénèse, de même que la fenêtre médiane chez *Rana esculenta* est un reste de la fente médiane de *Rana fusca*. Ensuite PEETERS dérive les suprarostralia des Ranidae de ceux d'*Alytes* qui ont les ailes séparées par une grande fente d'avec les saillies médianes, et il suppose que ces parties diverses s'unissent plus ou moins par du cartilage, en ménageant des ouvertures pour les vaisseaux sanguins. Cette dernière phrase est contraire à la réalité. En décrivant le deuxième stade d'*Alytes*, j'ai indiqué que *seul* le rameau *gauche* du R. palatinus peut être suivi jusqu'à la pièce médiane des suprarostralia et que le vaisseau de droite se ramifie déjà plus tôt. Le R. palatin de gauche se trouve sur la ligne *médiane* entre les deux saillies dorso-médiales des suprarostralia et non pas *latéralement*. Chez *Rana fusca* et *esculenta*, et selon PARKER (1881) chez quelques autres Ranidae (*R. pipiens*, *R. clamata*), les deux ouvertures sont du côté médial ou juste devant le point d'attache des suprarostralia aux cornets qui sont divergents comme chez la plupart des Anoures. En comparant les figures *a* et *d*, on voit claire-

[1] Cf. fig. 10 où les suprarostralia de *Rana fusca* sont dessinés d'après une figure de PEETERS.

[2] Le vaisseau sanguin remplit tout à fait l'orifice, dont la coupe transversale a la même dimension de celle d'une cellule cartilagineuse.

ment qu'on peut dériver la disposition chez *Alytes* de celle de *Rana fusca*, si on admet que la distance entre les points d'attache des suprarostralia est fort raccourcie. Les cornets d'*Alytes* qui sont à peu près parallèles, nous permettent d'énoncer cette supposition. Et à mon avis, il n'est pas impossible que l'atrophie de la partie distale du vaisseau sanguin droit soit en rapport avec cette disposition, puisque la divergence insignifiante des deux rameaux palatins chez *Alytes* pourrait être la cause que l'un des deux se charge de conduire le sang vers le tégument.

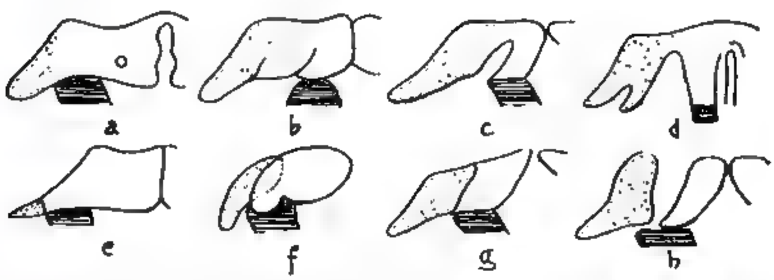

FIG. 10 *a-h*. — *Figures schématisées pour comparer les suprarostralia des Anoures suivants* : a) *Rana fusca* ; b) *Nototrema marsupiatum* ; c) *Calyptocephalus gayi* ; d) *Alytes obstetricans* ; e) *Pelobates fuscus* ; f) *Bufo lentiginosus* ; g) *Cyclorhamphus culeus* ; h) *Leptodactylus (ocellatus ?)*.

La deuxième série montre les suprarostralia pourvus d'une partie de l'aile qui est mobile. Les cornua trabeculae sont hachés et les parties de l'aile que l'ont peut comparer, sont pointillées.

Dans la figure *a* le for. pro art. palatina est indiqué à gauche et dans la fig. *d* la situation de l'arteria palatina, *médiane, non accouplée.*

Figures *a* et *d* selon PEETERS (1910) ; fig. *b*, *c*, *g* et *h* selon PARKER (1881) ; fig. *e* selon DUGÈS (1834) et SCHULZE (1892).

Donc les dispositions chez *Alytes* ne sont pas primitives.

Bien que la partie intertrabéculaire de la pièce médiane soit très raccourcie, la partie de l'aile est beaucoup plus développée et spécialisée chez *Alytes* que chez *Rana*. A cause de l'agrandissement de cette aile se forme la grande fente qui selon les figures de PARKER (1881, fig. 2 et 3, pl. 22) est aussi visible chez *Calyptocephalus gayi* (1). Même il est pos-

(1) Cf. ma figure 10*c* où je donne un dessin de ces suprarostralia d'après PARKER.

sible que cette partie devienne plus ou moins indépendante de la pièce médiane ([1]). Si les observations de PARKER sont exactes, on doit trouver cela chez *Cycloramphus culeus, Bufo lentiginosus* et surtout chez *Cystignathus* (*Leptodactylus ocellatus*). Et on est bien forcé de conclure d'après les descriptions de DUGÈS (1834) et de SCHULZE (1892) que chez *Pelobates* aussi la partie, à laquelle s'attache le ligament mandibulo-suprarostral (SCHULZE) ([2]), possède une certaine indépendance. DUGÈS qui l'appelle «adrostral», le considère comme un «appendice» du suprarostral, pourvu d'une «mobilité assez considérable» (pp. 85, 86 et pl. XIII, fig. 71 et 73). SCHULZE (1892, p. 7) décrit l'adrostral comme une petite pièce conique qui « mit der querabgestutzten Basis auf dem erwähnten Vorsprung des Suprarostrale beweglich aufsitzt ».

Quant au centre cartilagineux indépendant dans l'aile des suprarostralia qui apparaît le premier chez *Alytes* et les autres Anoures ([3]), il ne serait pas impossible que l'indépendance plus ou moins grande de ces pièces de cartilage latéral chez ces espèces, soit primitive. On pourrait donc dériver le développement de l'aile chez *Rana*, d'une réduction de celui d'*Alytes*. Une investigation plus complète qui tiendrait compte de l'attache des muscles et des ligaments, est désirable vu les données incertaines de PARKER et elle nous indiquerait dans quelle direction le développement a procédé. Car, bien que l'on puisse admettre la concrescence d'une partie de l'aile qui serait d'origine indépendante, suivie d'une réduction, on peut tout aussi bien admettre une spécialisation comme cause du grand développement de l'aile chez quelques espèces. Cette spécialisation serait l'effet de l'accomodation typique aux besoins du suçoir des larves.

([1]) Cf. ma figure 10 *a-h* où j'ai dessiné les suprarostralia des espèces qui seront nommés plus bas.

([2]) L'attache de ce ligament à l'adrostrale peut être comparé à l'attachez chez *Alytes* du ligament nommé à la partie dorsale de l'aile bifurquée des suprarostralia.

([3]) SPEMANN (1898) suppose que l'apparition précoce de ces parties latérales, auxquelles s'attachent les muscles, est une accomodation particulière.

F. Palatoquadratum, Cartilago Meckeli, Infrarostralia

Stade II

Il n'y a pas de connexion cartilagineuse entre le *palatoquadratum* et la capsule auditive, puisque le processus oticus, à proprement parler, manque. Le bout caudal du palatocarré est situé près de la partie de la paroi capsulaire, qui s'est un peu épaissie comme crista parotica, aux environs de l'ampoule du canal demicirculaire latéral. Une très étroite bande de tissu connectif sépare le palatoquadratum d'avec la crista, tandis que leurs plans de contact sont un peu aplatis l'un contre l'autre.

La connexion du palatoquadratum avec la paroi latérale par l'apophyse ascendante se trouve partiellement au-dessous de la partie la plus antérieure de la cupule antérieure. La commissure quadrato-craniale antérieure est large et porte une apophyse pseudo-ptérygoïdienne qui s'étend caudalement et offre une ouverture.

L'apophyse quadrato-ethmoïdale se continue en ligament quadrato-ethmoïdal qui s'unit devant la cavité nasale avec l'apophyse latérale du cornet trabéculaire.

Au bout caudal du palatocarré et à l'apophyse musculaire bien développée les muscles divers du squelette hyobranchial et de l'appareil mandibulaire prennent leur origine ([1]).

Au côté ventral du palatocarré le muscle ptérygoïdien et le muscle dépresseur postérieur de la mandibule sont situés l'un à côté de l'autre.

La position du *muscle ptérygoïdien* est médiale et ce muscle se détache du côté ventral de l'apophyse ascendante laquelle se prolonge jusqu'au-dessous de la capsule auditive, à laquelle elle s'attachera après la métamorphose.

L'attache de ce muscle se fait au coin rostro-latéral supérieur du cartilage de Meckel.

([1]) Pour la position relative des muscles on peut comparer fig. 2 et 11.

Le *muscle dépresseur postérieur de la mandibule* se trouve au côté latéral du muscle précédent, se détache de la partie du palatocarré qui est située en arrière de l'apophyse ascendante et s'attache au coin rostro-latéral inférieur du cartilage de Meckel. On peut considérer ces deux muscles comme antagonistes.

Le *muscle ptérygoïdien* s'élève dans la fenestra subocularis au-dessus du niveau du palatocarré et se place au côté médial du muscle temporal dans le même plan que lui ; vis-à-vis de l'apophyse musculaire, il croise ce muscle du côté ventral et se transforme en un tendon qui passe au-dessus de la partie articulaire du palatocarré et s'insère au cartilage de Meckel.

Le *muscle dépresseur postérieur de la mandibule* se trouve au côté ventral du palatocarré et croise à son côté dorsal le N. hyomandibulaire qui est compris entre eux sur une partie de son parcours. Etant situé médialement au muscle dépresseur du cartilage hyoïdien, il finit en face de la commissure quadrato-craniale antérieure en un tendon, qui court le long de l'articulation de l'hyoïde et du palatocarré et s'unit au cartilage de Meckel, latéralement au muscle dépresseur antérieur de la mandibule.

Le muscle dépresseur postérieur de la mandibule aide à la fonction du muscle antérieur (musc. depr. mand. de *Rana*) et puisqu'il manque chez *Rana* et *Bombinator*, j'ai dû lui donner ce nom.

Le muscle dépresseur de la mandibule (*Rana*) (ici le *muscle dépresseur antérieur*) prend son origine en partie au côté ventral du palatocarré près du bord antérieur de l'apophyse musculaire, en partie sur l'hyoïde. La première partie du muscle court d'abord au-dessus de la deuxième, mais bientôt elles s'unissent en s'attachant au côté ventral d'une petite saillie caudo-latérale du cartilage de Meckel. Le point d'attache du muscle dépresseur postérieur de la mandibule est situé juste devant ce point.

Le *muscle temporal* et le *muscle masseter* prennent leur origine du côté dorsal du palatocarré.

On peut distinguer dans la partie rostrale du muscle temporal deux groupes de fibres musculaires, dont le ventral est nommé par SCHULZE (1892) chez *Pelobates* : musculus subtemporalis. Chez *Alytes* les deux muscles commencent ensemble comme un seul muscle à la partie caudale du palatocarré près de la capsule auditive et de l'apophyse ascendante.

Avant de décrire les attaches de ces deux faisceaux musculaires, j'indiquerai encore deux muscles qui chez *Alytes* partent séparément du côté interne de l'apophyse musculaire (fig. 11) et s'apellent chez *Rana* tous deux : muscle masseter.

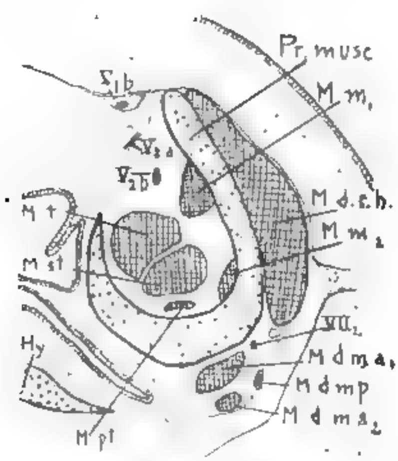

FIG. 11. — Coupe transversale d'une larve de 25 mm. (série 17) à travers le processus muscularis. Schématisée. Gross. 30×.

Position relative des muscles de l'appareil mandibulaire et de l'hyoid. *Hy.*, hyoid ; *M. d. c. h.*, musc. depressor cartilaginis hyoïdeae ; *M. d. m. a1*, musc. depressor mandibulae anterior (origo : quadratum); *M. d. m. a2*, musc. depressor mandibulae anterior (origo : hyoid.); *M. d. m. p.*, musc. depressor mandibulae posterior ; *M. m₁*, musc. masseter ? ; *M. m₂.*, musc. masseter; *M. pt.*, musc. pterygoïdeus ; *M. st.*, musc. subtemporalis ; *M. t.*, musc. temporalis ; *Pr. musc.*, proc. muscularis ; *V1b*, ramus externus narium V ; *V2a* et *V2b* ramus maxillaris superior et inferior (mandibularis) V; *VII2*, ramus hyomandibularis VII.

La partie dorsale du masseter s'unit surtout au muscle subtemporal, tandis que quelques fibres dorsales se trans-

forment bientôt en tendon et s'attachent avec le muscle temporal au cartilage de Meckel, juste au-dessus du point d'attache du paramandibulaire. De ce point une partie du tendon continue comme ligament mandibulo-suprarostral (SCHULZE) jusqu'à la saillie dorso-latérale de l'aile du suprarostral. La plupart des fibres du muscle dorsal s'unissent, comme je l'ai dit plus haut, au muscle subtemporal pour former un seul tendon qui s'attache à la saillie ventro-latérale de l'aile.

Je ne veux pas donner un nom définitif au muscle que j'ai nommé jusqu'à présent « partie dorsale du muscle masseter », avant qu'une étude comparative des muscles des mâchoires larvaires n'ait été faite. Car ce muscle qui disparaîtra pendant la métamorphose avec la partie de l'apophyse musculaire dont il se détache, est très probablement un muscle larvaire typique qui, par son point d'origine et d'attache, doit être distingué du véritable masseter, situé au côte ventral du premier.

Ce muscle masseter prend son origine un peu devant le susdit muscle dorsal et s'attache à la partie dorsale du cartilage de Meckel, derrière le muscle ptérygoïdien.

Le *muscle dépresseur du cartilage hyoïdien* se détache du côté latéral de l'apophyse musculaire.

La corbeille branchiale s'attache par un large groupe de muscles (musculi levatores arcuum branchialium) au bord latéral du palatocarré.

Le *cartilage de Meckel* est transversal par rapport au palatocarré. Outre les muscles indiqués, le *muscle submaxillaire* (qui ne se détache pas d'une pièce squelettique, mais commence indépendamment aux environs du tégument de la face ventrale) s'attache au cartilage de Meckel près de l'articulation des infrarostralia.

Le *muscle submental* ne s'est pas (ou pas encore) développé.

On peut distinguer au cartilage de Meckel deux parties : l'une, à peu près transversale, s'articule avec le palatocarré ; l'autre, plus courte, s'étend en avant en formant un angle obtus ; les infrarostralia s'unissent à cette dernière partie.

Les admandibularia sont à peu près parallèles à cette partie du cartilage de Meckel. Ce sont de petites lames cartilagineuses, placées verticalement, qui adhèrent par leur partie caudale au cartilage de Meckel, au point où celui-ci

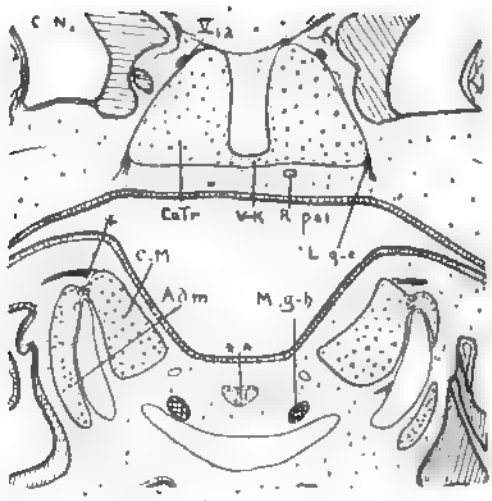

FIG. 12. — Coupe transversale d'une larve de 25 mm. (série 17) à travers les processus latérales des cornua trabeculae et les admandibularia. Gross. 40×.

Position des admandibularia. Le ramus palatinus droit de l'arteria carotis (dans la figure à gauche) est mal développé.

× Point d'attache du musc. temporalis et du musc. masseter (partie dorsale) au cartilage de Meckel. × × Infrarostralia, légèrement entamés par la coupe. *Adm.*, admandibulare ; *C. M.*, cartilago Meckeli ; *C. N.*, cavum nasi ; *Co. Tr.*, cornu trabeculae ; *L. q-e.*, ligamentum quadrato-ethmoïdale ; *M. g-h.*, musc. genio-hyoïdeus ; *V. K.*, cartilage, unissant les côtés ventraux des cornua; *V1a*, ramus internus narium V.

se recourbe en avant, sous l'insertion du muscle temporal (1). Le périchondre du cartilage de Meckel passe sur le bord dorsal des admandibularia qui sont forcés de suivre ses mouvements.

Entre les admandibularia et le cartilage de Meckel on trouve une cavité lymphatique ; c'est la continuation de la

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(1) Voyez pour un stade plus jeune : pl. VIII, fig. 3 et fig. 12.

grande cavité lymphatique ventrale. On y trouve aussi le N. mandibulaire V, qui suit le bord antérieur du cartilage de Meckel, descend entre ce cartilage et la partie distale des admandibularia et se ramifie pour innerver la peau et le muscle submaxillaire.

La connexion des *infrarostralia* avec le cartilage de Meckel se fait par un tissu connectif particulier ; une fente articulaire manque encore. Les infrarostralia s'unissent sur la ligne médiane par un tissu qui ressemble à du cartilage et se colore en bleu foncé par le bleu de Lyon. Les caractères de ce tissu seront discutés plus tard. A son côté ventral se trouve une copule très peu développée (longueur 0.075 mm.).

Les *muscles génio-hyoïdiens* qui se détachent du côté médial du cératobranchial IV, s'attachent au bord ventro-médial des infrarostralia.

Développement

La partie caudale du *palatocarré* n'est pas unie par un processus oticus à la capsule auditive ; pendant le développement ils se touchent, mais sans union cartilagineuse.

L'apophyse quadrato-ethmoïdale est, tout comme la pseudo-ptérygoïdienne, déjà cartilagineuse dans une larve de 2 $^1/_2$ mm. Pour la première fois on peut suivre le ligament quadrato-ethmoïdal jusqu'à l'apophyse latérale dans une larve de 16 mm. D'après la forme et la couleur des cellules cartilagineuses celle-ci ne doit exister que depuis peu.

Le *cartilage de Meckel* et les infrarostralia changent peu avant la métamorphose. Dans une larve de 7 ½ mm. ils sont déjà tous deux cartilagineux.

Les *infrarostralia* sont unis dès le début par un tissu connectif particulier. On peut retrouver ce tissu entre les hyoïdes : c'est la « pars reuniens » des hyoïdes. Il est caractérisé par une accumulation dense de noyaux et possède peu de substance intercellulaire, qui plus tard prend fortement le bleu de Lyon (en cela ce tissu diffère du cartilage normal, qui ne prend pas le bleu). L'orceïne donne une cou-

leur brun foncé à la substance intercellulaire de ce tissu [1].

Chez une larve de 25 mm. apparaît, dans la partie ventrale de ce tissu réunissant les infrarostralia, une petite pièce de cartilage. Sa position correspond à celle de la copule II des hyoïdes qui siège dans le tissu de la pars reuniens. La copule entre les infrarostralia est de forme ronde en coupe transversale.

La chondrification des admandibularia se fait dans des larves de 12 1/2 à 16 mm.

Littérature

Le processus oticus de *Rana fusca* (GAUPP, 1893) se forme par condensation du tissu qui unit le bord postérieur du palatocarré à la capsule auditive. Ce tissu se chondrifie non seulement à partir du palatocarré, mais aussi à partir de la capsule.

Quoiqu'on ne puisse pas distinguer chez *Alytes* un processus oticus proprement dit, on pourrait donner ce nom à la partie caudo-latérale du palatocarré, située contre la capsule auditive, et on pourrait la comparer au processus oticus des Urodèles qui, selon PEETERS, ne s'unit pas par du cartilage à la capsule auditive. *Alytes* n'est pas la seule espèce parmi les Anoures où le processus oticus soit faiblement ou pas du tout développé (cf. p. ex. les pl. 22 et 30 de PARKER, 1881). En certains cas, où le processus oticus est peu développé, la crista parotica a pris de grandes dimensions et peut s'unir à lui (PARKER,1881; pl. 17, fig. 1, 2, 5 et 6 ; *Leptodactylus ocellatus*). Au contraire la crista parotica d'*Alytes* est peu développée.

Le ligament quadrato-ethmoïdal de *Rana* se développe tôt (larve de 14 mm.) et précède la formation de l'apophyse quadrato-ethmoïdale (larve de 25 mm. - 30 mm.), contrai-

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[1] C'est pourquoi il est possible de colorer en couleur de contraste le tissu de la pars reuniens des hyoïdes. La couleur brun-foncé de la substance intercellulaire se distingue très clairement dans les coupes transversales parmi le cartilage non-coloré des hyoïds.

rement à *Alytes*, où cette dernière apparaît d'abord. Selon PARKER ce ligament semble se chondrifier chez *Pseudis* et délimite avec l'apophyse latérale du cornet trabéculaire un orifice ovalaire.

L'apophyse pseudo-pterygoïdienne de *Rana* apparaît assez tard, selon GAUPP chez des larves entre 29 mm. et la métamorphose ; selon PEETERS, déjà chez une larve de 29 mm. Elle existe déjà chez des larves d'*Alytes* de 16 mm. Parfois l'apophyse pseudo-ptérygoïdienne se développe considérablement (*Pseudis paradoxa*, *Calyptocephalus gayi*); parfois elle manque (*Leptodactylus*, *Hyla*, *Nototrema*, *Acris* et d'autres, PARKER, 1881).

Il n'y a pas lieu de comparer ici les muscles qui se détachent du palatocarré et qui font fonctionner l'appareil mandibulaire des larves. Une révision de la nomenclature est fort à désirer, pour la larve et pour l'adulte.

GAUPP (1893) a observé que les infrarostralia de *Rana fusca* sont unis par une copule de cartilage hyalin. Dans une larve de 14 mm. (selon PEETERS déjà plus tôt) une bande de tissu les unit, qui se chondrifiera bientôt. Ce cartilage, chez *Rana esculenta*, existe dans une larve de 6,5 mm. (PEETERS, 1910). La description de GAUPP permet de douter qu'il ait observé chez *Rana fusca* le développement du cartilage de la copule dans le tissu qui unit les infrarostralia qu'il distingue cependant. PEETERS, au contraire, décrit la formation de la copule, qui s'unit des deux côtés par du cartilage « plus faible » aux infrarostralia. La preuve que PEETERS parle ici du même cartilage remarquable que chez *Alytes*, c'est qu'il dit (p. 157) : « door zyne kleinere overlangs gestrekte cellen en later bovendien door zyn donkerder kleur, blyft het tot na de metamorphose scherp onderscheiden van het kraakbeen der infrarostralia zelf ». Les caractères de ce cartilage sont très distincts par les méthodes de coloration au bleu de Lyon et à l'orceïne [1]. La réaction vis-à-vis de ces matières

[1] J'ai appliqué le bleu de Lyon comme l'éosine. Les préparations restent peu de temps dans une solution de bleu de Lyon dans l'alcool à 96 % ; puis elles sont lavées à l'alcool à 96 % et transportées dans

colorantes est la même que celle du tissu de la pars reuniens des hyoïdes. Tous deux ont une couleur jaunâtre à la lumière directe, tandis que le cartilage des hyoïdes et des infrarostralia est blanc.

Il est possible que, vu la couleur jaune du tissu, les cloisons cellulaires contiennent une substance élastinoïde. Ce n'est pas cependant du cartilage élastique proprement dit, car un fin lacis de fibres élastiques manque totalement (¹).

Jusqu'à quel point pourrait-on comparer la copule des infrarostralia avec la petite pièce de cartilage impaire qui unit chez *Xenopus* les deux cartilages de Meckel ? C'est le développement qui le montrera. RIDEWOOD (1898) qui appelle ce cartilage de *Xenopus* « basimandibulare » le compare au basihyale et le considère comme primitif et donnant par subdivision les infrarostralia pairs. GAUPP (1906), en comparant la copule de *Rana* avec le basimandibulaire de *Xenopus*, ne suit pas le raisonnement de RIDEWOOD. Car ici se pose la question : à quoi faut-il comparer les infrarostralia eux-mêmes ? PARKER, dans ses dessins de *Xenopus*, donne toujours dans des stades divers deux infrarostralia et parle (p. 630) de la : « interposition of a pair of short, terete, inferior labials ». Cette donnée de PARKER n'est probablement pas exacte (²) J'ai trouvé chez une larve de *Xenopus* (avant

l'alcool absolu, etc. On peut varier la concentration de la solution du bleu de Lyon selon le besoin. J'ai employé l'orceïne de la façon suivante : de l'orceïne à 1 % dans de l'alcool à 96 % auquel on a ajouté 1 % H. Cl. UNNA (Encyclopaedie der Mikr. Technik, 1903, p. 193) a recommandé cette coloration pour l'élastine.

(¹) Les opinions sur les caractères de la pars reuniens des hyoïdes sont divisées. STOHR (1882) l'a décrite le premier et la considère comme étant du cartilage. GAUPP (1893 et 1906) la tient pour du cartilage jeune, non développé. RIDEWOOD (1898) parle de : « a dense mass of whitish fibrous tissue » ; chez *Microhyla* cette substance lui fait décidément l'impression de cartilage. Après ce que je viens de dire, il est clair que ce tissu est vraiment du cartilage, quoiqu'il soit d'un caractère spécial.

La connexion de la copule avec les hyoïdes par ce tissu à la fois ferme et mobile est fort intelligible, quand on pense aux mouvements des hyoïdes par la contraction du muscle sous-hyoïdien.

(²) Il est possible également que les infrarostralia de *Xenopus* se forment séparément dans les stades jeunes et qu'ils confluent plus tard.

la métamorphose : longueur totale, 67 ½ mm., pattes postérieures, 5 mm.) une pièce cartilagineuse, transversale, courbée et impaire, qui à mon avis, représente, d'après sa forme, les deux infrarostralia et non pas la copule de *Rana* et *Alytes*.

Si l'on ne trouvait chez les Anoures, comme *Rana*, *Alytes* et d'autres, point de copule, l'hypothèse de Ridewood serait plus vraisemblable. Mais puisque la copule existe en fait, il vaut mieux supposer que les infrarostralia ne sont que des parties du cartilage de Meckel et qu'on peut comparer la copule avec le basihyale, comme Gaupp (1893) l'a déjà fait.

Selon Parker (1876) il n'y a pas de copule chez *Pipa* ni d'infrarostralia [1]. On peut admettre que l'existence des infrarostralia est en rapport avec la vie larvaire, spécialement avec le suçoir des Anoures.

V. RÉSUMÉ DES RÉSULTATS ACQUIS CHEZ ALYTES

1. La tête des Anoures contient un segment de moins que celle des Urodèles. Par conséquent il est très probable que le plan basal se compose seulement de *deux* composants : le plan trabéculaire et le plan occipital. Cette opinion est appuyée par le fait que le cartilage « mésotique » n'a jamais été démontré ni défini chez les Anoures. Chez les Urodèles, au contraire, il est très net.

Chez *Alytes* les deux composants se chondrifient en même temps, de sorte qu'il n'est pas possible de prouver la séparation de l'arc occipital, comme chez *Rana* (Peeters, 1910).

2. Pendant le développement il y a une limite entre le plan basal et le cartilage de la capsule auditive ; le plan basal ne prend aucune part à la formation du bord médial de la fenêtre ovale primaire.

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[1] Pour les Urodèles c'est la même chose.

3. Vu la position de l'arc occipital des Anoures par rapport aux segments, il est très probable que cet arc correspond à l'arc préoccipital des Urodèles et que par conséquent l'atlas des Anoures correspond à l'arc occipital des Urodèles.

4. Le développement de l'arc occipital se fait, contrairement à celui de *Rana fusca*, avant le développement de la première vertèbre.

5. L'arc occipital se développe en partie à partir du plan basal, en partie à partir de la capsule auditive.

6. La crista occipitalis lateralis manque dans les stades jeunes, mais finit par se développer aussi bien que chez *Rana*.

7. La corde dorsale ne s'étend pas jusqu'à l'infundibulum, par suite d'une réduction très précoce. Entre eux persiste un grand espace qui se réduit dans la suite, mais ne disparaît jamais. C'est pourquoi le plan trabéculaire impair peut se former immédiatement devant le bout de la corde et se chondrifie, sans que le bout extrême soit forcé de se réduire, comme chez *Rana*.

8. La réduction du reste de la corde se fait en trois parties, dont la première phase s'achève avant la métamorphose. Le mode de réduction de cette partie et du revêtement cartilagineux des côtés dorsal et ventral sont les mêmes que chez *Rana fusca*.

9. Le premier cartilage de la capsule auditive ne se développe pas comme d'habitude autour du canal demicirculaire latéral, mais bien à partir de deux centres : les cupules antérieure et postérieure. A partir du premier centre, le cartilage continue en direction caudale autour du canal demicirculaire latéral ; à partir du deuxième centre, l'organe auditif se recouvre de cartilage à son côté médio-ventral ; ce cartilage s'unit ensuite au plan basal.

10. La partie de la paroi médiale de la capsule auditive, qui est située au côté caudal du trou acoustique se développe la première.

11. Le trou acoustique est divisé secondairement en trous acoustiques antérieur et postérieur par une cloison qui ne

se trouve pas dans le même plan que la paroi médiale de la capsule auditive, mais qui se dresse plus en dedans.

12. Il existe un rapport entre le développement du recessus partis basilaris et la présence ou l'absence d'un trou périlymphatique externe. Chez les Urodèles et parmi les Anoures chez *Pipa* (et *Xenopus* ?) ce recessus est peu ou pas développé ; là on trouve seulement le trou périlymphatique interne. Chez les Anoures phanéroglosses comme *Rana*, *Alytes*, etc., ce recessus est bien développé chez la larve ; alors l'orifice externe est ménagé dans la capsule auditive.

L'orifice périlymphatique interne est le plus ancien phylogénétiquement. Les deux trous périlymphatiques sont des orifices préformés et ils ne sont pas dus à la subdivision d'un seul orifice, situé dans la paroi capsulaire médiale, comme les trous périlymphatiques antérieur et postérieur d'*Hynobius*.

13. Le trou périlymphatique accessoire manque chez *Alytes*.

14. Le nerf facial entre avec le N. VIII dans la capsule auditive et perfore la paroi capsulaire médio-ventrale. Secondairement ce N. VII est enfermé dans un canal, dont la partie la plus antérieure, extra-capsulaire, est constituée par le plan basal et la paroi de la capsule auditive, tandis que la partie la plus grande, intracapsulaire, est formée par le revêtement cartilagineux du nerf à l'intérieur de la capsule.

15. Le canal demi-circulaire postérieur se sépare le dernier d'avec la cavité de la capsule auditive, par une cloison cartilagineuse. Il est très probable que ce septum sera apparu le dernier dans la phylogénie et cela non seulement à cause de ce développement tardif, mais aussi parce que le canal latéral membraneux se sépare le dernier dans l'ontogénie ; en outre, le septum peut manquer chez quelques Urodèles, soit individuellement, soit constamment.

16. L'union cartilagineuse du palatocarré et de la capsule auditive par le processus oticus ne se fait pas avant la métamorphose. Quoique le bout caudal du palatocarré s'applique étroitement contre la capsule auditive, ils restent toujours séparés par une bande de tissu très mince.

17. La crista parotica ne se développe que faiblement avant la métamorphose.

18. Le tectum posterius des Anoures représente probablement un tectum synoticum. L'arc occipital ne prend pas part à sa formation, contrairement à ce que l'on voit chez les Urodèles, où le tectum posterius peut être considéré comme un tectum interoccipitale.

19. Il n'y a pas de taenia tecti medialis chez *Alytes.*

20. Les taeniae tecti marginales ne sont pas libres chez *Alytes.* Pour cette raison le nom « cristae marginales » est plus conforme à la réalité.

21. Le premier cartilage de l'opercule apparaît dans le pourtour inférieur et caudal de la fenêtre ovale. On a des raisons d'admettre que l'opercule est une partie de la paroi de la capsule auditive et est apparu dans la phylogénie plus tard que la columelle (pars interna plectri).

22. L'opercule des Anoures phanéroglosses se chondrifie plus tôt que le plectrum, contrairement à l'opercule (pars opercularis) des Urodèles.

Chez les Anoures aglosses (*Pipa* et *Xenopus*) ce n'est pas le cas ; un opercule libre manque, même chez la larve. Néanmoins il est possible qu'une étude plus précise montre qu'on peut distinguer à l'os auditif desAglosses une pars opercularis.

23. La chondrification des trabécules, et probablement aussi leur formation, procèdent en direction caudo-rostrale, contrairement à ce qui se passe chez *Rana.* Il est vraisemblable que cette formation procède à partir du plan parachordal.

24. La paroi latérale se développe três tôt, en direction rostrale, comme un rebord latéral, assez large, en s'unissant au pilier de la paroi latérale. Cette bande cartilagineuse *latérale,* qu'on ne peut pas appeler « dorsale Randspange », s'unit près de la commissure quadrato-craniale antérieure à la partie du trabécule qui se relève vers le haut.

25. Contrairement à *Rana,* le trou du N. oculomoteur n'est pas immédiatement limité, avant que le cartilage de la paroi soit développé complètement, mais il le fait beaucoup plus tard, à des stades voisins de la métamorphose. Pour cela la

cloison des trous des N. II et III s'accroît en direction caudale. Cette cloison se développe très probablement en même temps à partir du rebord latéral de la paroi et à partir du trabécule.

26. Le cartilage de la paroi latérale pousse en haut à partir du rebord latéral et limite alors la cavité cranienne sur son côté dorso-latéral.

27. Dans cette paroi latérale on trouve devant le trou du N. IV un orifice, par lequel une branche de la veine jugulaire entre dans la cavité cranienne. Cet orifice disparaît pendant la métamorphose.

28. Le trou du N. IV peut se trouver chez des larves en métamorphose dans le fronto-pariétal en même temps que dans la paroi latérale cartilagineuse.

29. La base du crâne se forme en direction caudale, à partir du plan internasal (celui-ci apparaît, contrairement à *Rana*, après la chondrification du plan trabéculaire impair) et aussi en direction médiale à partir des trabécules.

Le trou carotidien est entouré par du cartilage avant le trou cranio-palatin ; la partie située au-dessous de l'hypophyse se chondrifie la dernière, mais avant la métamorphose.

La chondrification de la base cranienne se fait de différentes manières.

30. Le foramen prooticum se forme par l'union cartilagineuse de la paroi latérale avec la capsule auditive. Cet arc cartilagineux se continue dans les cristae marginales et apparaît après la chondrification de la paroi latérale.

31. Le plan précérébral ne possède pas de fenêtre précérébrale ; il se développe à partir du plan internasal et des petites saillies cartilagineuses sur les cornets.

32. Le canal du R. interne des narines V est limité par la paroi latérale et le processus antorbitalis, tandis que sa voûte se chondrifie indépendamment.

33. Les cornets trabéculaires s'allongent en direction orale pendant leur développement et sont à peu près parallèles. Latéralement ils s'élargissent en apophyses latérales, qui manquent chez *Rana*, mais existent chez nombre d'Anoures et auxquels s'attachent les ligaments quadrato-ethmoïdaux.

34. Les parties caudales des cornets sont unies par leurs faces ventrales par une solide bande de cartilage (l'homologue du ligament intertrabéculaire inférieur de *Rana*) ; ce cartilage se prolonge en direction rostrale en un ligament qui s'attache, après s'être bifurqué, aux extrémités des cornets. Sur leurs côtés dorsaux les parties proximales des cornets s'unissent aussi sur une courte étendue par du cartilage.

Le ligament intertrabéculaire supérieur se trouve aux extrémités des cornets ; il s'étend en direction latérale sur les suprarostralia.

35. Les suprarostralia se forment après les trabécules et se joignent aux rudiments des cornets. Plus tard, les suprarostralia se séparent des cornets par une mince bande d'un tissu qui se colore par le bleu de Lyon.

36. Les suprarostralia ne sont pas séparés pendant leur formation. La chondrification se fait à partir d'un centre situé latéralement et à partir d'une partie qui se joint aux cornets, tandis que la pièce médiane se chondrifie la dernière.

37. Il est impossible de dériver les suprarostralia de *Rana fusca* de ceux d'*Alytes* par la méthode de PEETERS, à cause de la position médiane du rameau palatin gauche de l'artère carotide. Celui-ci peut être suivi jusqu'à la pièce médiane des suprarostralia, tandis que le rameau droit se termine plus tôt. La disposition chez *Alytes* est due à la divergence minime des cornets et par conséquent au raccourcissement de la pièce médiane des suprarostralia.

38. Il faut expliquer les grandes ailes des suprarostralia d'*Alytes*, soit par une spécialisation considérable (et alors elles sont issues des petites pièces de cartilage correspondantes de *Rana*), soit par la concrescence de la pièce médiane, bifurquée ou non (qui doit être dérivée des cornets trabéculaires), avec des pièces de cartilage latérales, indépendantes, comme PARKER les a vues chez quelques Anoures. Dans ce dernier cas on peut se figurer que la disposition chez *Rana* est dérivée des ailes d'*Alytes* par réduction. La chondrification précoce du cartilage latéral des suprarostralia peut étayer cette hypothèse.

39. Le palatocarré se chondrifie en direction rostrale et ne possède point de processus oticus bien développé qui l'unirait à la capsule auditive.

40. Le processus pseudo-pterygoïdeus est pourvu d'un orifice aux stades avancés.

41. Le ligament quadrato-ethmoïdal se développe après l'apophyse quadrato-ethmoïdale.

42. Outre le muscle dépresseur de la mandibule (qui existe aussi chez *Rana*), *Alytes* possède un muscle, se détachant de la partie caudale du palatocarré, que j'ai nommé, en raison de sa fonction et de sa position « musculus depressor mandibulae posterior ». Le muscle, situé à la partie rostrale du crâne s'appelle par conséquent « musculus depressor mandibulae anterior ».

43. Un muscle indépendant existe au côté interne de l'apophyse musculaire au dessus du muscle masseter ; il a son propre point d'attache au cartilage de Meckel et au suprarostrale. Une étude comparative devra démontrer, si ce muscle fait partie du muscle masseter ou non.

44. Outre le susdit muscle et le muscle masseter, les muscles suivants s'attachent au cartilage de Meckel: lemuscle ptérygoïdien et les deux parties du muscle temporal ; le ligament mandibula-suprarostral s'y insère aussi.

45. Les admandibularia (paramandibularia, PEETERS) même en formation, sont situés contre le cartilage de Meckel et sont plus tard unis à lui par du périchondre.

46. Les infrarostralia qui, pendant leur formation, formaient un tout avec le cartilage de Meckel, s'unissent entre eux par un tissu qui montre les mêmes propriétés que le tissu de la pars reuniens des hyoïdes. Il se colore par le bleu de Lyon en bleu foncé, par l'orceïne en brun foncé, tandis que le cartilage reste incolore. A cause de ces réactions qui caractérisent les fibres élastiques et à cause de la structure et de l'aspect de ce tissu (*jaunâtre*, contrairement au cartilage *blanc*), on peut admettre que ce tissu d'union est une espèce particulière de cartilage, dont les cloisons intercellulaires contiennent une substance élastinoïde.

47. Une copule, normalement cartilagineuse, se montre dans ce tissu chez les larves plus développées. Probablement on ne peut pas la comparer à la pièce cartilagineuse, impaire qui unit les mandibules chez *Xenopus*. La copule des Anoures phanéroglosses correspond par sa position au basihyale qui réunit les hyoïdes entre eux.

L'étude du développement du chondrocrâne d'*Alytes obstetricans* a mis en évidence des analogies et des différences, plus ou moins importantes, avec *Rana fusca*. Je signale en premier lieu *Rana fusca* parce que jusqu'à présent cette espèce est la mieux connue. Le développement rapide de la partie caudale, ou la formation retardée de la partie rostrale du crâne, sont en rapport avec ces différences, dont j'indiquerai les suivantes : la chondrification simultanée des deux composants du plan basal ; le développement de l'arc occipital avant celui de la première vertèbre et par conséquent l'absence originelle de la crista occipitalis lateralis ; la chondrification des trabécules, procédant en direction orale ; la formation du plan internasal après celle du plan trabéculaire non apparié ; le développement rapide du rebord latéral avant que le trou du N. oculomoteur et le trou prootique soient entourés de cartilage et la formation retardée et impaire des suprarostralia. Donc la chondrification chez *Alytes* procède généralement en direction rostrale, contrairement à ce que l'on voit chez *Rana*.

Outre quelques propriétés qui dénotent une spécialisation plus élevée, comme la bifurcation de l'aile des suprarostralia et l'existence d'un plus grand nombre de muscles (1), il y a aussi des différences, causées par la réduction du chondrocrâne. Ceci le rapproche parconséquent de la disposition du chondrocrâne chez les Urodèles, sans être pourtant primitif. Car Gaupp a déjà signalé que le chondrocrâne des Anoures est, par sa formation, plus riche en cartilage, plus primitif

(1) Excepté le musculus depressor mandibulae posterior, je puis nommer le musculus infrabranchialis du squelette hyobranchial que Peeters (1910) a décrit le premier.

que celui des Urodèles à certains égards. Chez *Alytes*, l'absence d'une taenia tecti medialis est remarquable sous ce rapport ; et il faut y ajouter probablement aussi l'absence d'un processus oticus.

Mais en deux points *Alytes* se montre plus primitif que *Rana* : le trajet intracapsulaire du N. VII et l'existence des admandibularia. On voit aussi le N. VII entrer avec le N. VIII dans la capsule auditive chez plusieurs Urodèles. C'est une disposition primitive, vu la relation étroite qui existe dès l'origine entre ces deux nerfs et vu le trajet analogue du N. VII chez *Petromyzon*. L'existence des admandibularia rappelle les cartilages labiaux des Sélaciens ou les paramandibularia des Dipneustes.

Deux propriétés qui étaient jusqu'à présent caractéristiques des Urodèles, apparaissent aussi chez les Anoures : le parcours intracapsulaire du nerf facial et la perforation par le N. trochlearis des fronto-parietalia.

Au contraire, deux dispositions des Anoures : l'existence de deux trous périlymphatiques et la formation de l'opercule avant la pars interna plectri n'existent pas chez *Pipa americana* parmi les Anoures aglosses ; à cet égard ceux-ci se rapprochent plutôt des Urodèles que des Anoures phanéroglosses.

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EXPLICATION DES PLANCHES VIII ET IX

ABRÉVIATIONS EMPLOYÉES

A. occ.-v. = arteria occipito-vertebralis.
Adm. = admandibulare.
Arc. occ. = arcus occipitalis.
C. aud. = capsula auditiva.
C. M. = cartilago Meckeli.
C. qu.-cr. a. = commissura quadrato-cranialis anterior.
Ch. d. = chorda dorsalis.
Co. Tr. = cornu trabeculae.
Cr. ma. = crista marginalis.
F. car. = foramen caroticum.
F. cr.-pal. = foramen cranio-palatinum.
F. jug. = foramen jugulare.
F. ov. pr. = fenestra ovalis primaria.
F. pr. = foramen proöticum.
G. V, X. = ganglion du nerf V ou X.
G. B. = vésicule auditive.
Gl. pr. = ganglion proöticum.
I. A. = artère intersegmentale.
Infrar. = infrarostrale.
K. S. II = segment céphalique II (ou : rudiment du myotome, provenant du segment céphalique II).
L. W. = rebord de la paroi latérale.
M. o. = musculi oculi.
O. K. = cartilage de la capsule auditive.
O. P. = ébauche du cartilage de la capsule auditive.
Oc. = oculus.
Occ. P. = ébauche de l'arc occipital.
P. K. = cartilage parachordal.
P. P. = ébauche du cartilage du plan parachordal.
P. q. = palatoquadratum.
Pl. bas. = planum basale.
Pl. T. = planum trabeculare.
Pr. asc. = processus ascendens.

Pr. lat. = processus lateralis.
Pr. musc. = processus muscularis.
Pr. ps.-pt. = processus pseudo-pterygoïdeus.
Pr. q.-ethm. = processus quadrato-ethmoïdalis.
R. S. 1, 2, 3. = 1°, 2°, 3°, segments du tronc (ou myotomes, appartenants aux susdits segments du tronc).
Sp. 1, 2, 3. = nerfs spinaux, 1, 2, 3.
Suprar. = suprarostrale.
T. syn. = tectum synoticum.
T. V. = saillie de la trabécule.
Tr. = trabecula.
V. J. = vena jugularis.
Zw. = paroi latérale.
Zw. K. = cartilage de la paroi latérale.
Zw. P. = pilier de la paroi latérale.
II. = nervus opticus.
V^1. = ramus orbito-nasalis du nerf V.
V^2. = ramus maxillo-mandibularis V.
VII^1. = ramus palatinus VII.
VII^2. = ramus hyomandibularis VII.
IX. = nervus glosso-pharyngeus.
X. = nervus vagus.
X^1. = nervus occipitalis.

Toutes les figures se rapportent à *Alytes obstetricans*, excepté le schéma 2. Les figures 5-13 sont demi-schémiques.

Le matériel d'*Alytes* m'a été remis fixé et retiré de ses enveloppes ; je ne puis pas indiquer la longueur de l'animal au moment où il quitte cette enveloppe. Je ne puis donc distinguer entre l'embryon et la larve, et c'est toujours ce dernier mot que j'emploierai.

PLANCHE VIII.

FIG. 1. — *Chondrocrâne d'une larve de 7 mm.* (série 9), d'après un modèle en cire. Vu du côté dorsal. Gross. 50×.

Le cartilage de la paroi latérale n'est pas représenté à droite. Les suprarostralia et une partie de l'arc occipital sont encore en état procartilagineux et indiqués par une couleur moins foncée. La limite entre la capsule auditive et le plan basal est pointillée. N. V^1 et V^2 ne sont pas indiqués. × Tissu médian, unissant les suprarostralia ; il n'est pas distinctement limité. × × Tissu, unissant les infrarostralia, non cartilagineux. × × × Tissu procartilagineux du côté dorsal de la corde.

FIG. 2. — *Le même chondrocrâne, vu du côté ventral.* Grossissement 50×. Les admandibularia sont encore procartilagineux et pas encore indiqués.

FIG. 3. — *Chondrocrâne d'une larve de* 32 *mm. longueur totale ; longueur des membres postérieurs* 3 *mm.*, d'après une préparation totale (fixation : acide picro-sulfurique ; coloration : bleu de méthylène. Vu du côté dorsal. Gross. 16×.

Par l'enlèvement du cerveau, il n'était plus possible de constater le degré de développement de la partie centrale de la taenia tecti transversalis. La partie de la base du crâne légèrement colorée, est encore du cartilage très jeune. Le cartilage de Meckel, les infrarostralia et les admandibularia sont omis, pour que le dessin soit clair.

FIG. 4. — *Même chondrocrâne, vu du côté ventral.* Gross. 16×.

La fenêtre ovale et le for. perilymphaticum externum sont invisibles à cause de la coloration intense de la capsule auditive. × Point, où le N. VII apparaît en quittant la capsule auditive. Par une erreur de retouche la place du processus pseudo-pterygoïdeus à droite est inexacte. Celui-ci se trouve en effet au-dessous du plan du palato-carré, comme je l'ai indiqué à gauche.

PLANCHE IX.

Dans les figures 5-14, je ne veux pas désigner par K. S. II et R. S. 1, 2, 3, le dernier segment céphalique ou les trois premiers segments du tronc, mais je veux dire les myotomes, développés partiellement ou entièrement, qui leur correspondent. Cette notation est employée dans un but d'abréviation.

FIG. 5 et 6. — Coupes horizontales d'une larve de 4,5 mm. (série 2). Gross. 35×.

Situation du dernier myotome céphalique partiellement développé, et du premier myotome du tronc par rapport à la vésicule auditive, au N. X et à l'artère occipito-vertébrale.

FIG. 7 et 8. — Coupes horizontales d'une larve de 5 mm. (série 3). Gross. 35×.

Disposition des myotomes de la tête et du tronc comme dans les figures 5 et 6.

FIG. 9. — Coupe horizontale d'une larve de 5 mm. (série 4). Gross. 35×.

Disposition de l'ébauche de l'arc occipital par rapport au premier myotome du tronc qui est en réduction.

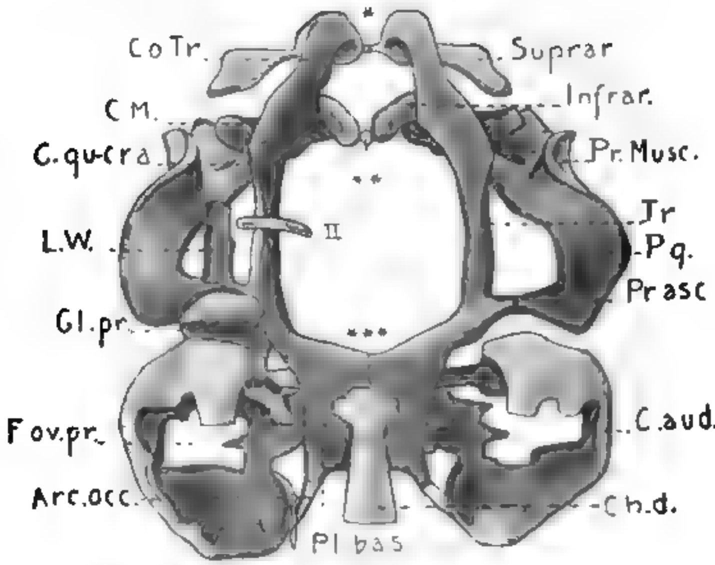

Fig. 1

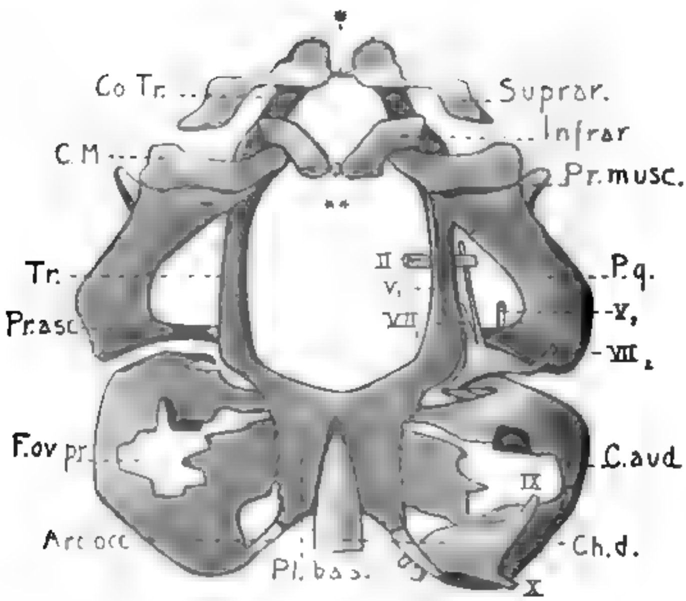

Fig. 2

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Planche VIII.

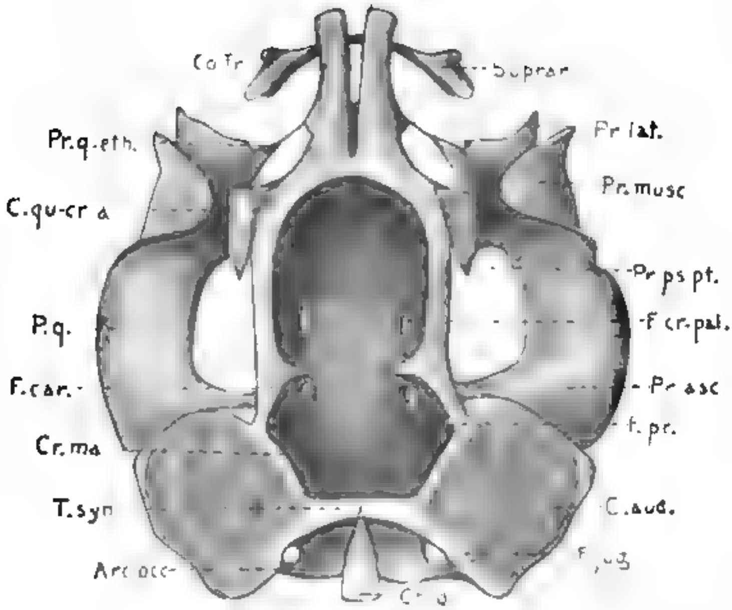

Fig. 3

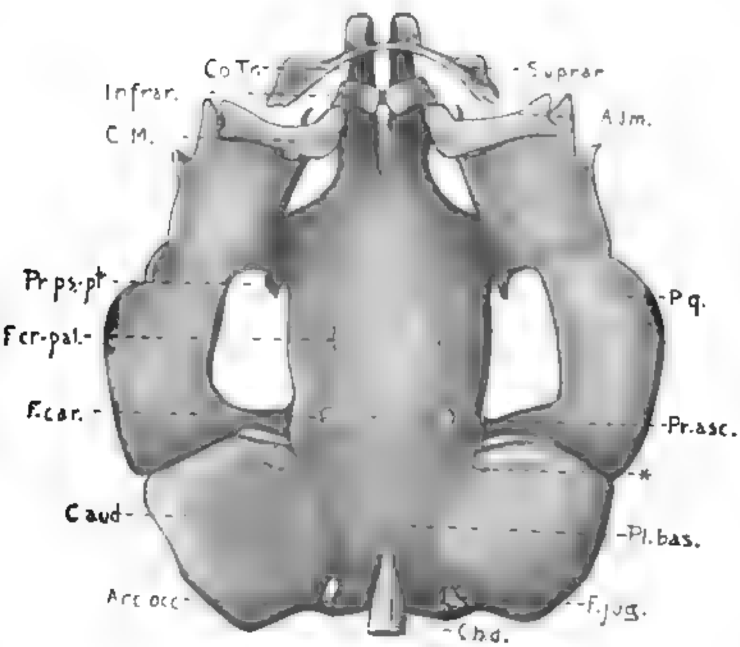

Fig. 4

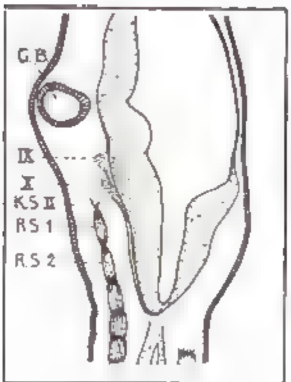

FIG 5

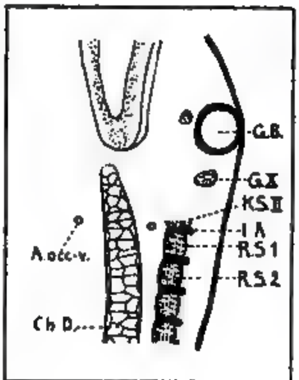

FIG. 6

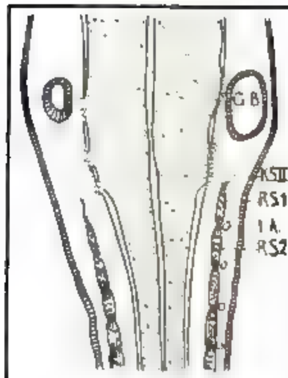

FIG. 7

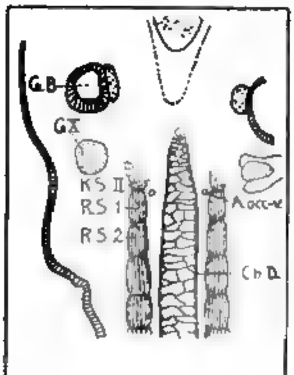

FIG. 8

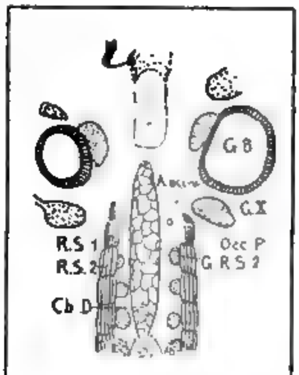

FIG. 9

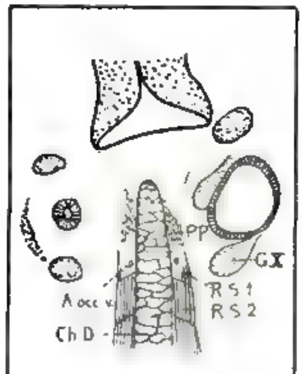

FIG. 10

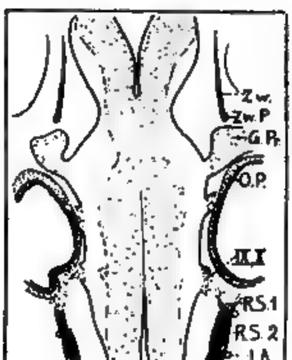

FIG. 11

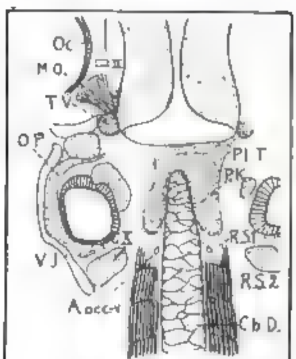

FIG 12

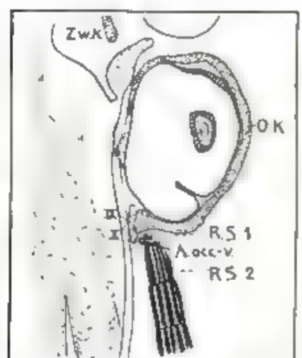

FIG. 13

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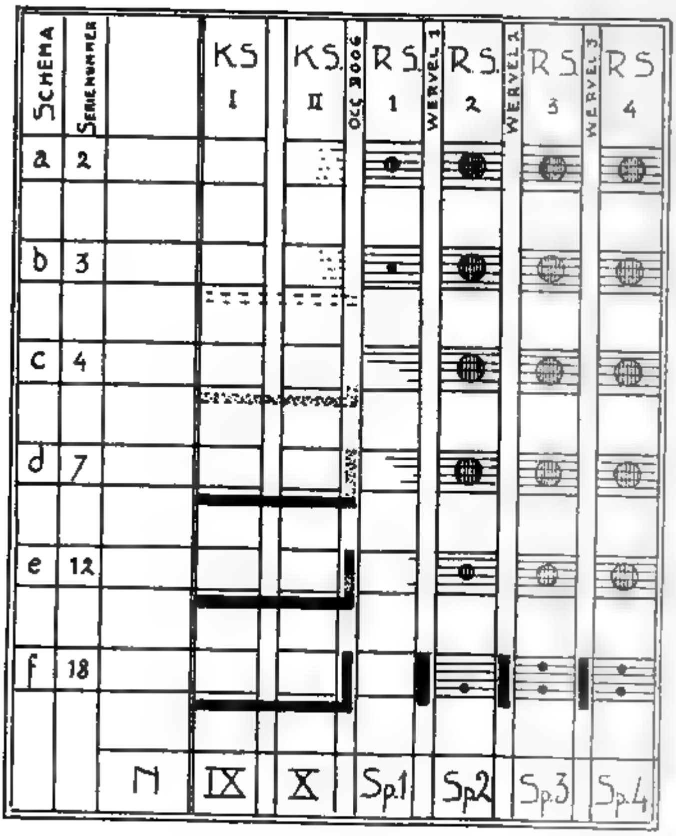

Schéma 1

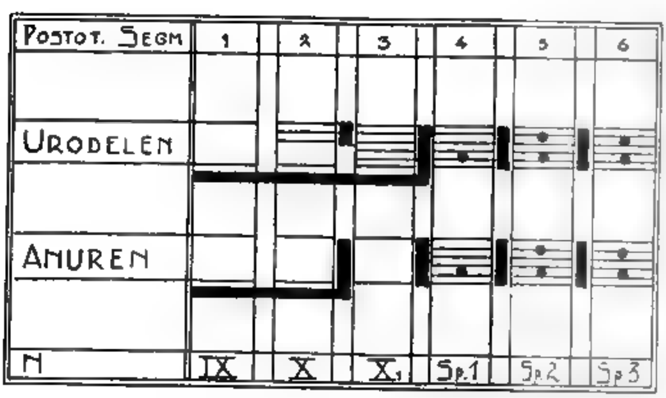

Schéma 2